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# AN INTRODUCTION TO CYTOLOGY

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# AN INTRODUCTION TO
# CYTOLOGY

BY
LESTER W. Ryland SHARP, 1887-
*Cornell University*

"The most important discoveries of the laws, methods and progress of nature have nearly always sprung from the examination of the smallest objects which she contains, and from apparently the most insignificant enquiries."—Lamarck, *Philosophie Zoologique.*

SECOND EDITION

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TO
MY FATHER

# PREFACE TO THE SECOND EDITION

In rewriting this book an attempt has been made to enhance its usefulness by bringing it more nearly down to date, and by removing some of the more obvious defects of the first edition. Among the topics which recent advances have made it profitable to treat more fully than before are the cytology of hybrids, polyploidy, apomixis, the achromatic figure, the Golgi material, and animal spermatogenesis. These and other alterations have necessitated a considerable increase in the length of the text and the number of illustrations, many of the latter replacing figures in the previous edition. The bibliography, though more compact in form, has been greatly augmented.

A noteworthy departure will be recognized in the reliance on the Organismal Theory as a fundamental concept: the primary emphasis has been placed upon protoplasm and the organism as a whole rather than upon the cell as such. This has profoundly affected the manner of presenting a number of important topics; and it should, in our opinion, prove of service in developing truer perspectives in biological thought.

In addition to Agar's *Cytology, with Special Reference to the Metazoan Nucleus* and Doncaster's *An Introduction to the Study of Cytology*, which appeared as the first edition of this book went to the press, several subsequent treatises have facilitated the preparation of the present revision. Special mention should be made of A. Meyer's *Analyse der Zelle*, Tischler's *Allgemeine Pflanzenkaryologie*, Lundegårdh's *Zelle und Cytoplasma*, Schürhoff's *Die Plastiden*, the volume on *General Cytology* edited by E. V. Cowdry, and the third edition of Wilson's *The Cell in Development and Heredity*.

The author gratefully acknowledges the assistance which has materially lightened the task of revision. He is deeply indebted to Professor Victor Grégoire, Professor Otto Rosenberg, Professor B. F. Kingsbury, Professor C. E. McClung, Professor A. C. Fraser, Dr. William Seifriz, Dr. R. H. Bowen, Dr. E. V. Cowdry, and Dr. L. F. Randolph, who have examined various portions of the manuscript. He is no less grateful to the many others—especially his associates in the Department of Botany at Cornell University—whose helpful discussions and criticisms have contributed notably to the revision of the book.

L. W. S.

ITHACA, NEW YORK,
*January*, 1926.

# PREFACE TO THE FIRST EDITION

This book has been prepared for students of the biological sciences who desire a means of becoming more readily acquainted with the literature and problems of cytology. It does not pretend to be an exhaustive treatise for the use of experienced cytologists, though it is hoped that to them also some of its features may be of service.

For a number of years students of biology, especially those working along botanical lines, have been faced with the task of searching through a widely scattered literature for information on various cytological subjects. It is the purpose of this book not to render the consultation of that literature unnecessary, but only to make it easier; the student can scarcely be too strongly urged to derive his information from original sources wherever possible. The author does not presume to replace, but rather aims to supplement, Professor Wilson's well-known book, *The Cell in Development and Inheritance*, which, though written twenty years ago and with the emphasis primarily on the zoölogical side, will remain invaluable to all workers for many years to come. The more recent works of Gurwitsch (*Morphologie und Biologie der Zelle*), Heidenhain (*Plasma und Zelle*), and Buchner (*Prakticum der Zellenlehre*) are of importance, especially to the zoölogist.

The living cell, or protoplast, which represents an organized protoplasmic unit of structure and function, obviously cannot receive complete description in structural terms. Until a comparatively recent period cytological researches dealt primarily with cell structure, including particularly the conspicuous changes undergone by this structure in connection with the reproduction of the cell (cell-division) and of the multicellular organism (maturation and fertilization). A gradual shifting of emphasis has since led to the opening of fruitful fields in other directions, and the important results already achieved have shown with increasing clearness the need for a closer acquaintance with the physiological aspects of cell activity, not only in metabolism and growth, but also in the reproductive phases of the life cycle. The present work, though dealing mainly with the structural aspects of the subject, may aid indirectly in fulfilling the above need by making the prerequisite data of cell morphology more readily available.

Throughout the book, which in many of its chapters treats chiefly of the plant cell, attention is focussed upon the protoplast; the cell wall is given only brief consideration, since it plays a relatively minor rôle in the processes of particular interest to the cytologist at the present time.

Because of their fundamental importance in connection with the problems confronting the geneticist, the phenomena of nuclear division, chromosome reduction, and fertilization are described with considerable fullness, and their relation to the problems of heredity is taken up in five special chapters. With regard to many of the subjects treated, it has not been found possible to formulate final conclusions, since in many cases nothing more than tentative general statements are warranted by the facts in our possession. In some chapters little more than catalogs of conflicting opinions can be given, but in such a form the state of certain questions is not inaccurately represented. The student entering upon the field of cytology will be impressed by the large number of special points which remain undetermined and general questions which await adequate answers. If he can look upon cytology as a developing science, and if he has reached the stage at which he no longer demands categorical answers to all his questions, this book will be of interest to him as much for the problems it raises as for those it helps to solve. Not the least of its functions is to indicate lines of research along which he can hope to make contributions to the subject.

In compiling his materials the author has not hesitated to draw very freely upon the writings of others. In many cases where direct quotation is not made, the language of the originals has been closely followed in order to lessen the likelihood of misrepresentation. His great debt to Professor Wilson's book will be apparent to all those familiar with that admirable work. The majority of the diagrams and a number of the other figures are new. Most of the latter, however, have been redrawn from works cited in the text, not only that the value of the book may be enhanced by the presence of authoritative illustrations, but also that the student may be encouraged to become more familiar with the original papers. The general systematic positions of organisms indicated in the text by their scientific names only may be ascertained by referring to the generic names in the index.

The illustrations are largely the work of Miss Mildred Stratton, in whose skill and spirit of coöperation the author has had invaluable assistance. The criticisms of the text kindly given by Professor C. J. Chamberlain of the University of Chicago and Professor R. A. Emerson of Cornell University have been very highly appreciated. Acknowledgments are also made to the author's other colleagues for their advice and continued encouragement. Further criticisms looking toward the improvement of future editions will be welcomed.

L. W. S.

Ithaca, New York,
*September* 8, 1920.

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# AN INTRODUCTION TO CYTOLOGY

## INTRODUCTION

In a survey of the evolution of biological science it is observed that, while diverging lines of inquiry have broadened the field of view, the attention of investigators, speaking generally, has been directed in turn to successively smaller constituent parts of the organism. For many years plants and animals were studied chiefly as wholes. But very early there began to be made many scattered observations on the various organs and tissues composing the body, and from these relatively crude beginnings morphology and histology arose. Again, when the protoplasmic mass which we know as the cell came to be regarded as an important structural and functional unit, it became evident that the problems it presents should be investigated to a certain extent by themselves, and such investigation has since been looked upon as the chief task of modern cytology.

It is scarcely adequate, however, to say that cytology is simply the study of cells. There are many tissues and many complex organisms which show no actual cellular subdivisions, yet they carry on the same vital activities and confront the biologist with nearly all of the same fundamental problems as do the cellular forms. The cytologist, therefore, has to deal primarily with the structural organization and functional differentiation of protoplasm, which may or may not exist in the form of what are ordinarily called cells. Hence cytology may be defined in general terms as that branch of biology which treats of the organization of protoplasm, usually in the form of cells, and the relation of alterations in this organization to such phenomena as growth, differentiation, and heredity. In the following chapters attention will be devoted first to protoplasm and later to cells; this we conceive to be the order of their importance.

From this point of view the traditional distinction between cytology and histology as branches of biology which deal with cells and with tissues respectively becomes much less clear. Both of these subjects, moreover, since they treat chiefly of structural features which can be observed with the microscope, have long been rather sharply set apart from physiology, to which has been left the investigation of processes not so observable. But it must be recognized that such a division of biological phenomena is purely arbitrary. Every process involves a structural alteration of some order in the protoplasmic substratum. Were our microscopes capable of revealing masses of molecular and atomic dimensions, we should doubtless find that structural and functional changes are actually but one series of changes regarded in two ways; they are two aspects of one reality.

In the course of cytological research there arise many questions immediately concerned with interactions of molecules and atoms, so that from one standpoint biochemistry may be regarded as a division of cytology, just as from another it appears as a division of chemistry. Indeed, the advisability of setting any of these branches of science very sharply apart with definitions may be questioned, for the conception of the fundamental unity of the diversified phenomena with which they are all in some measure concerned is unquestionably one of the utmost value in biological thought, and should never be allowed to become obscured by useful but arbitrary distinctions. Cytology thus occupies an interesting position in natural science; it stands with physics and chemistry on one hand and with the complex phenomena peculiar to living organisms on the other. The more perfect integration of the results of inquiries in these several fields will depend not only upon further acquisitions within the field of cytology, but also upon the measure in which physiologists, morphologists, physicists, and chemists recognize the truly complementary nature of their tasks.

## CHAPTER I

## HISTORICAL SKETCH

Cytology is almost wholly a development of the last 75 years. Before protoplasm had come to be recognized as the physical basis of life, and the cell as essentially a protoplasmic unit, cytology as we know it scarcely existed, although important investigations of the structure and development of plants and animals had been in progress for many years. The course later followed by the growing science was so profoundly affected by these early investigations that it will be found advisable to review them rather fully. Furthermore, it will be seen that the discovery of the cellular organization of most organisms, and the formulation of an influential theory based on the cell as a unit of primary importance in development, long antedated a proper conception of the true significance of protoplasm. As a result, cytology has not only derived its name from the cell, but has been dominated by the cell concept from the first, notwithstanding the ever-increasing evidence that the characteristic activities of living organisms are fundamentally reactions of protoplasmic systems, which may or may not possess what is ordinarily regarded as cellular organization. This latter point of view, according to which cells are subordinate though highly important units in organic differentiation, has gained adherents rather slowly, and it will lend perspective to our account to indicate at the outset a current renewal of the tendency thus to transfer the principal emphasis from the cell to protoplasm.

The investigation of such protoplasmic structures as nuclei and plastids was begun nearly a century ago, long before their constitutional relationship was suspected, but most of our knowledge of these and other kindred elements has been acquired during the past 50 years. The last quarter of the nineteenth century witnessed an intensive study of the behavior of cells, nuclei, and chromosomes in the various processes involved in the growth and differentiation of the organism. Among the noteworthy results of this study was the theory that the phenomena of inheritance are in some way closely dependent on the activities of the nucleus, a theory which received striking support after the principles of Mendelian heredity were rediscovered in 1900. This rediscovery has very largely determined the character of cytological research so far in the present century. It has brought cytology into intimate association with genetics and taxonomy, while a renewed study of living protoplasm has resulted in similar alliances with physiology and biochemistry. One of the most conspicuous and encouraging tendencies of the present day is to be recognized in this closer correlation of the various subdivisions of biology.

**The Discovery of the Cellular Organization of Plants and Animals.**—Prior to the seventeenth century attempts to analyze the structure of organisms had only limited success. Aristotle (384–322 B.C.) in his *De Partibus Animalium* distinguished the "homogeneous parts" and the "heterogeneous parts," the former corresponding in general to what are classified as tissues (bone, fat, cartilage, flesh, blood, lymph, nerve, membrane, nails, hair, skin, vessels, tendon, etc.), and the latter to the larger members of the body (head, face, hands, feet, trunk, etc.). Theophrastus, the pupil and successor of Aristotle, taught in his *Historia Plantarum* that the plant body is composed of "sap," "veins," and "flesh." Aristotle's classification was developed further by Galen (131–201 A.D.) and his followers. Although the above components are no longer regarded as elementary parts, but rather as tissues and organs, the ancients may be pardoned for not carrying the analysis further, for they did not possess the necessary instruments. Something was then known about the refraction of light, but it was not until many centuries later that suitable lenses were available. The first compound microscope was produced in 1590 by J. and Z. Janssen, spectacle makers of Middleburg, Holland, and during the first part of the seventeenth century other improved models were designed by other workers. These instruments in the hands of men possessing scientific curiosity soon led to many significant discoveries. A new world was opened to the eye of science, and the compound microscope has since remained an instrument of extraordinary value in biological research.

The first description of the cellular organization of plants was given in 1665 by Robert Hooke (1635–1703), a resident of London. Hooke, who is said to have been a man of eccentric appearance and habits, showed a remarkably varied activity, being at one time or another professor of geometry, architect, and curator of experiments to the Royal Society. His interest in optics led him to examine all sorts of objects with the compound microscope. In charcoal and later in cork and other plant tissues he found small honeycomb-like cavities which he called "cells." He had no distinct notion of the cell contents, but spoke of a "nourishing juice," which he inferred must pass through pores from one cell to another. His many observations were embodied in his *Micrographia* (1665), a large work illustrated with 38 plates. The chapter containing his remarks on cells is entitled "Of the schematisme or texture of cork and the cells and pores of some other such frothy bodies." Quaint and crude as it now appears to us, the *Micrographia* will always be of special interest because it was the earliest work to deal with cells, which became the subject matter of a new science.

Three other names even more prominent in the early history of microscopy are those of Grew, Malpighi, and Leeuwenhoek.

Nehemiah Grew (1641–1712) was an English physician and botanist. He began a careful study of plant structure in 1664, and in 1670 read his first important paper before the Royal Society. Further contributions followed at intervals until 1682, when all of them were published under the title *The Anatomy of Plants*. Like Malpighi, an abstract of whose first work on plants was presented to the Royal Society in 1671, Grew was interested in tissues, and gave particular attention to the combinations of these tissues in different plant organs. He was strongly impressed by the manner in which the cells, which he also called "vesicles" and "bladders," appeared to make up the bulk of certain tissues: ". . . the parenchyma of the Barque," he said, "is much the same thing, as to its conformation, which the froth of beer or eggs is, as a fluid, or a piece of fine Manchet, as a fixed body" (p. 64). He further believed the walls of the cells to be composed of numerous extremely fine fibrils: in the vessels or longitudinal elements these fibrils were wound in the form of a close spiral, while the vessels themselves were bound together by a transverse series of interwoven threads. He accordingly compared the structure of the plant with that of a basket, and with "fine bone-lace, when the women are working it upon the cushion" (p. 121).

Marcello Malpighi (1628–1694), an Italian physiologist and professor of medicine at Bologna, Pisa, and Messina, is best known for his important pioneer work in anatomy and embryology. Most of his observations on plants were included in his *Anatome Plantarum* (1675) and had to do largely with the various kinds of elements making up the body of the vascular plant. A clear foreshadowing of the Cell Theory is seen in his remarks concerning the importance of the "utriculi" in the structure of the body. At Pisa Malpighi was associated with G. A. Borelli, who was one of the first to use the microscope on the tissues of higher animals.

Antony van Leeuwenhoek (1632–1723) of Delft is remembered for his pioneer researches in the field of microscopy. He constructed a number of simple lenses of high power, and with these he was able to see for the first time certain Protozoa, bacteria, and other minute forms of life. In the course of his investigations he observed the cells ("globules") in the tissues of higher organisms. His work, in spite of the fact that it was carried on without any definite plan, brought to light a number of important facts, but in general his accomplishments do not bear favorable comparison with those of Grew and Malpighi, the founders of plant anatomy.

**Preformation and Epigenesis.**—After the death of Leeuwenhoek there ensued a period during which the actual investigation of the structure of organisms remained practically at a standstill. But there was considerable indulgence in speculation, which should be recorded here, not because it can be regarded as scientific cytology, but because of the influence it exerted upon the formulation of many cytological problems in later years. This speculation resulted in the division of the biologists of the day into two schools, the main controversy being over the manner in which the embryo develops from the egg. The two theories formulated in answer to this question have been called the Preformation Theory and the Theory of Epigenesis.

According to the Preformation Theory, the basis for which was laid in the seventeenth century works of Swammerdam, Malpighi, and Leeuwenhoek, the egg contains a fully formed miniature individual, which simply unfolds and enlarges as development proceeds. Because of this unfolding the theory was also known as the Theory of Evolution, an expression which has a quite different connotation today. In the eighteenth century the preformation idea was carried to an absurd extreme by Bonnet (1720–1793) and others, who argued that if the egg contains the complete new individual the latter must in turn contain the eggs and individuals of all future generations successively encased within it, like an infinite series of boxes one within another. This theory of encasement (*emboîtement*) was a logical deduction from the since abandoned premise that everything, including organisms for all time, had been formed by one original creation, and that nothing could therefore be formed anew. The preformationists soon became separated into two groups: the spermists, or animalculists, and the ovists. By the former the new individual was supposed to be encased in the spermatozoön, and figures were actually published showing a small human figure, or "homunculus," within the sperm head. The ovists, on the contrary, held that the individual is encased in the egg. A bitter strife was carried on over this question by the two groups of preformationists, and various interesting compromises were made. But all extreme forms of preformationism were to disappear in the light of more critical investigations, which went far to support the opposing Theory of Epigenesis.

Two of the early champions of the Theory of Epigenesis were William Harvey (1578–1667; *Exercitationes de Generatione Animalium*, 1651), and Caspar Friedrich Wolff (1733–1794; *Theoria Generationis*, 1759). As the result of many careful observations on the embryogeny of the chick, Wolff was able to show beyond question that development is epigenetic: neither egg nor spermatozoön contains a formed embryo; development consists not in a process of unfolding, but in "the continual formation of new parts previously non-existent as such" (Wilson). Here was room for the principle of true generation, or "the production of heterogeneity out of homogeneity." The *Theoria Generationis* is to be regarded as one of the really great contributions to biological science, for the Theory of Epigenesis, to which it furnished substantial support, later became established with modifications as a fundamental principle of embryology, particularly through the work of von Baer in the nineteenth century.

In commenting on preformation and epigenesis Whitman (1894) emphasizes the fact that the tendency of modern biology has not been to show the entire falsity of either of these views, but to seek out the germs of truth possessed by each, and to relate them to modern biological conceptions. "The two views missed the mark by over-shots in contrary directions," says Whitman. The one theory claimed too much preformation; everything was preformed at the start. The other theory claimed too much postformation; everything was formed anew. Our present position, although it excludes both views in their crude original form, involves in a new sense both conceptions. When we say that the egg is organized, possessing an architecture or mechanism in its cytoplasm or nucleus which largely predetermines development, we are making a modernized statement of the preformation idea. When we say that the parts of the individual are in no way delineated in the egg, but are mainly determined by external conditions during the course of development, we are speaking in terms of modern epigenesis. "The question is no longer whether all is preformation or all postformation; it is rather this: *How far is postformation to be explained as the result of preformation, and how far as the result of external influences?*" When it is borne in mind, therefore, that one of the outstanding problems of modern cytology is that of identifying the factors involved in the development of an organized and highly differentiated individual from an organized but relatively undifferentiated egg, it is at once evident that any sketch of cytological history would be incomplete without some reference to the early Theories of Preformation and Epigenesis.

**The Renewal of the Study of Organic Structure.**—The researches of Hooke, Grew, and Malpighi in the seventeenth century had made it apparent that "cells," or "globules," are important structural elements in organisms. When attention was again directed to such matters toward the end of the eighteenth century, a number of interesting suggestions were offered regarding the origin and significance of these elements.

One of the earliest theories of cell-formation was that which had been put forward by Wolff in the *Theoria Generationis* (1759). According to Wolff, every organ is at first a clear, viscous fluid with no definite structural organization. In this fluid, cavities (Bläschen; Zellen) arise and become cells, or, by elongation, vessels. These may later be thickened by deposits from the "solidescible" nutritive fluid. The cavities, or cells, are not to be regarded as independent entities; organization is not effected by them, but they are rather the passive results of an organizing force (*vis essentialis*) inherent in the living mass. Three important points in Wolff's theory should be noted because of the relation they bear to subsequent conceptions of the rôle of cells: the spontaneous origin of the cell, the organization of parts by differentiation in the homogeneous living mass, and the passive rôle of the cell in this organizing process.

K. Sprengel (1766–1833) stated that cells originate in the contents of other cells as granules or vesicles which absorb water and enlarge. Sprengel's observations seem to have been very poorly made, for he evidently mistook starch grains for the "vesicles" which were supposed to grow into new cells. But Sprengel's theory was upheld by L. C. Treviranus (1779–1864) in a work appearing in 1806, and both men fought many years for its support. Kieser (1812) further developed the theory that granules in the latex are "cell germs" which later hatch in the intercellular spaces to form new cells.

With a much clearer understanding of the nature of the problems involved, a number of excellent observations were made by J. J. Bernhardi in 1805, by H. F. Link and K. A. Rudolphi in 1807, and by J. J. P. Moldenhawer in 1812. It is to be regretted that the deserved attention was not given to their results, for they promised to lead in the right direction. A number of years later Mirbel, in a work on *Marchantia* (1831–1833), distinguished three modes of cell-formation: the formation of cells on the surface of other cells, the formation of cells within older cells, and the formation of cells between older cells. The first mode apparently represented the budding of the germ tube arising from the spore, while the second and third modes were formulated as the result of a misinterpretation of the process of cell-multiplication in growing gemmæ. Between 1830 and 1840 several other botanists, including Dumortier, Morren, Meyen, and von Mohl, observed the division of cells, chiefly those of certain algæ. The work of Hugo von Mohl (1805–1872) is particularly noteworthy, since it was he who contributed the first careful description of cell-division. That this was a regular mode of cell origin, however, was not realized until some years later.

Because of their relation to the Cell Theory, which is soon to be discussed, special consideration should be given the views of J. B. P. Lamarck (1744–1829), C. F. Mirbel (1776–1854), and H. J. Dutrochet (1776–1847). As recently emphasized by Gerould (1922), certain aspects of the Cell Theory were taught in Paris at the opening of the nineteenth century, 40 years before Schleiden and Schwann published their epoch-making works.

The famous French biologist, Lamarck, in his *Philosophie Zoölogique* (1809), strongly emphasized the fundamental importance of "cellular tissue" in the structure and development of organisms. In his own words, " . . . cellular tissue is the matrix in which all the organs of living bodies have been successively formed, and . . . the movement of fluids through it is nature's method of gradually creating and developing those organs out of this tissue" (Elliott's translation, p. 230). He adds in a footnote that he had been teaching this doctrine since 1796. With regard to the internal structure of plants, he says: " . . . all that we can find is, among the simplest, a cellular tissue without vessels but variously modified and stretched or compressed according to the special shape of the plant; and in the more complex, an assemblage of cells and vascular tubes of various sizes, mostly with lateral pores, and a varying number of fibers, resulting from the compression and hardening that a portion of the vascular tube has undergone" (p. 235). His assertion that the universal basis of all organization is such cellular tissue, without which no living body could continue to exist, is obviously an overstatement.

As Gerould points out, Lamarck's cellular tissue theory, like his theory of evolution, was not supported by a body of well-authenticated published facts. It was rather Mirbel (1808), Lamarck's colleague, who furnished such observational data. Special notice should be taken of the fact that by both men it was cellular tissue, and not the individual cell, that was regarded as fundamental. Both looked upon the organism as a cellular whole, rather than an association of elementary unicellular organisms. Reference will be made to this point further on in connection with later theories involving cells.

It was Dutrochet (1824) who contributed the idea of the individuality of the cell. "This astounding organ," he states, ". . . . is truly the fundamental element of organization; everything, indeed, in the organic tissues of plants, is evidently derived from the cell, and observation has just proved to us that it is the same with animals." The embodies essentially the central idea of the theory later put forward by Schleiden and Schwann; but Dutrochet, in common with his contemporaries, apparently regarded as "cells" a variety of small globules visible in tissues under the microscope. The cell was not yet a "standardized" unit, and little progress could be made until such a unit had been more clearly defined.

A notable contribution was now made by Robert Brown (1773–1858). Brown is famous chiefly for his great taxonomic monographs and for his morphological work, but he is known in cytology as the man who is usually given the credit for the discovery of the nucleus, which he announced in 1831. Although it was he who was impressed by the probable importance of the nucleus, concluding in 1833 that it is a normal cell element, certain other observers, notably Fontana, who described a nucleus in 1781, and Meyen, who saw it in *Spirogyra* in 1826, should share the honor for its discovery. After Brown's announcement, observations on nuclei in various tissues multiplied rapidly; and as it became evident that cells of widely different types possess one nucleus each, the cell as an individual unit stood out clearly from the other elements with which it had long been confused. The formulation of a general theory based on the cell unit was now possible.

**The Foundation of the Cell Theory.**—The year 1838 marks an epoch in the history of biology. In this and the following year Schleiden and Schwann founded the Cell Theory, which had an enormous influence upon all branches of biological science. Cells had been observed by various workers during a period of many years, and had been recognized as being constantly present in the bodies of living organisms, but it remained for Schleiden, and especially Schwann, to formulate a comprehensive theory based on the cell as a standard elementary unit.

Matthias Jakob Schleiden (1804–1881) is one of the most prominent and interesting characters in botanical history. He studied law at Heidelberg, medicine at Göttingen, and botany at Berlin, where he met Schwann and Robert Brown. The association of these men undoubtedly meant much to the future of botany and zoölogy. Eventually Schleiden became Professor of Botany at Jena, where he remained for 23 years. He became famous not merely because of his own work, but chiefly as the result of the tremendous impetus which he gave to investigation. He sought to place botany on a scientific footing equal to that of physics and chemistry, and insisted upon accurate observation and developmental studies as bases of morphology. Sachs says: "Endowed with somewhat too great love of combat, and armed with a pen regardless of the wounds it inflicted, ready to strike at any moment, and very prone to exaggeration, Schleiden was just the man needed in the state in which botany then was."

Theodor Schwann (1810–1882) was associated, as a student, with Johannes Müller, the great physiologist, first at Würzburg and later at Berlin. It was in the latter place that he put forth his statement of the Cell Theory. Immediately afterward he went to Louvain, where he remained as professor for nine years, later transferring to Liége. In disposition he contrasted strongly with Schleiden, being described as "gentle and pacific."

It is said that Schleiden, while dining with Schwann, discussed with him some of his ideas regarding cells in plants which he had been studying in his laboratory. Schwann had been making similar observations on animals, and after the meal the two went to Schwann's laboratory, where they came to the conclusion that cells are fundamentally alike in both kingdoms. Schleiden's treatise on the subject, *Beiträge zur Phytogenesis*, appeared in 1838. In the opening paragraphs he says: " . . . every plant developed in any higher degree is an aggregate of fully individualized, independent, separate beings, even the cells themselves. Each cell leads a double life: an independent one, pertaining to its own development alone; and another incidental, in so far as it has become an integral part of a plant. It is, however, easy to perceive that the vital process of the individual cell must form the first, absolutely indispensable fundamental basis, both as regards vegetable physiology and comparative physiology in general . . ."

It was Schwann, however, rather than Schleiden, who formulated the Cell Theory in a comprehensive manner. He announced it in concise form in 1838, and in 1839 published a very full account under the title "*Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen.*" In this classic work a great variety of animal cells are carefully described and figured, and the cell stands forth as an individual unit with a clearness unapproached in any earlier treatise. With regard to the general significance of cells Schwann says: "The elementary parts of all tissues are formed of cells in an analogous, though very diversified manner, so that it may be asserted *that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells* . . . All organized bodies are composed of essentially similar parts, namely, of cells . . . The whole organism subsists only by means of the reciprocal action of the single elementary parts." And further: "The development of the proposition that there exists one general principle for the formation of all organic productions, and that this principle is the formation of cells, as well as the conclusions which may be drawn from this proposition, may be comprised under the term *Cell Theory* . . ."

Now it must be carefully noted that the essential point in the Cell Theory of Schleiden and Schwann was that cells, no matter how diverse they may be in appearance, are all morphologically equivalent, and are elementary living units whose action determines the development of the organism; the cell is *the primary agent of organization.* We have too often allowed the observable fact that most bodies are composed of cells and their products, and the further fact that the life cycles of such organisms may be described as cell-successions, to stand as a statement of the Cell Theory, forgetting that the theory lies rather in the conception of the cell individual as the leader in the development of organic structure and in function. It is here that the views of Schleiden and Schwann differed from those of their French predecessors. With Lamarck and Mirbel, even as with Wolff, cells were not very definitely individualized, and were more or less passive in the formation of organs in the fundamental cellular matrix—theirs was a Tissue Theory rather than a Cell Theory. With Schleiden and Schwann, on the other hand, cells were definite elementary organisms primarily responsible for the development and activity of the body. Dutrochet seems to have been the only one to approach this conception previously, but, as has been seen, he was hampered by the lack of a standard by which to judge the nature of the units he observed. We shall be better able to compare the relative merits of the theories of Lamarck and Schwann after the Organismal Theory has been discussed in subsequent pages.

Since Schleiden and Schwann so strongly emphasized the importance of cell-formation, it will be of interest to describe the process by which they supposed new cells to arise. Schleiden was responsible for the curious interpretation; in fact, his *Beiträge zur Phytogenesis* dealt largely with the origin of cells. Robert Brown had recently discovered the nucleus, and about it Schleiden built up his theory of "free cell-formation," which was essentially as follows. In the general cell contents or mother liquor ("cytoblastema") there are formed, by a process of condensation, certain small granules (later called "nucleoli" by Schwann). Around these many other granules accumulate, thus forming nuclei ("cytoblasts"). Then, "as soon as the cytoblasts have attained their full size, a delicate transparent vesicle appears upon their surface." This vesicle in each case enlarges and forms a new cell, and, since it arises upon the surface of the cytoblast (nucleus), "the cytoblast can never lie free in the interior of the cell, but is always enclosed [*i.e.*, imbedded] in the cell wall . . ." Cell-formation was thus regarded as endogenous ("cells within cells") rather than the result of cell-division. Without this erroneous idea of the origin of cells Schleiden and Schwann might have elaborated their theory still further. But this was to be the work of their successors.

**Elaboration of the Cell Theory.**—The Cell Theory was at once widely adopted as a fundamental proposition in biological research, though in certain aspects it underwent considerable modification as knowledge increased. It was especially desirable to clear up the matter of cell origin, and to this task a number of men, among whom may be mentioned Hugo von Mohl (1805–1872), F. J. F. Meyen (1804–1840), Franz Unger (1800–1870), and Carl von Nägeli (1807–1891), addressed themselves. As has already been pointed out, the multiplication of cells by division was observed by several investigators between 1830 and 1840, von Mohl being the first to describe the process in some detail.

Meyen apparently made the first attempt (1837–1839) to distinguish cell-division from the free cell-formation described by previous workers. It has been pointed out by Sachs that if this short step had been clearly taken earlier the peculiar theory of cell-formation later developed by Schleiden would have been impossible. Von Mohl had also made observations ruling out Schleiden's idea, but his excessive caution prevented him from making a decisive statement on the subject. In two works (1835, 1844) he maintained that there are two methods of cell-formation: by division and by the formation of cells within cells. He thought the "primordial utricle" (protoplast) must be absorbed to make way for the two new ones, or, less probably, the old one must divide into two. Like Schleiden, he thought the nucleus must be incorporated in the cell wall, but later (1846) he concluded that it lies in the primordial utricle. It was in his paper of 1846 that von Mohl introduced the term "protoplasm" in its present sense. Unger (1844) in two papers on vegetable growing points and the growth of internodes also argued for the origin of cells by division.

Nägeli (1844) produced an exhaustive treatise on the nucleus, cell-formation, and growth. In algæ and the microsporocytes of angiosperms he clearly showed that cells multiply by division, and Schleiden was forced to admit that this might be "a second kind of cell-formation." The continuation of Nägeli's researches in 1846 completely overthrew Schleiden's conception of free cell-formation, establishing the significant fact that practically all vegetative cell-formation is by cell-division. Many similar observations had been made by Unger and von Mohl, but Nägeli elaborated a broad theory which took into account all of the data at hand. He distinctly defined cell-division and free cell-formation, and showed that what had been taken for the latter might be regarded as a special case of the former. Nägeli's conclusions were supported by new evidence furnished by other investigators, who further held that not only vegetative cells, but also those reproductive cells (in thallophytes) which Nägeli thought in some cases might be formed freely, originate by a modified process of cell-division. It now seemed clear to these men that cells arose only from preëxisting cells, a conception which had been emphasized by Remak (1841), and which Virchow (1855) expressed in the dictum "*omnis cellula e cellula*." This dictum is frequently employed today, but it is obvious that some qualifications should be made for the origin of cells in plasmodial masses.

Opinions concerning the origin of the nucleus and its rôle in cell-division varied greatly among these workers, reliable observations being as yet insufficient to allow any definite conclusion. In 1841 Henle believed with Schleiden and Schwann that the nucleus was formed by the aggregation of "elementary granules," and that it was not constantly present. Von Kölliker in 1845 asserted that nuclear division precedes the division of the cell. Remak, as a result of his observations on blood cells in the chick embryo, formulated a definite theory of cell-division (1841, 1858). He believed cell-division to be a "centrifugal" process; the nucleolus, nucleus, cytoplasm, and cell membrane were supposed to divide in turn by simple constriction. Just such a process, though evidently very exceptional, has been observed at a more recent date by Conklin (1903). In describing a case of nuclear division Wilhelm Hofmeister (1824–1877) stated that the membrane of the nucleus dissolved, the nuclear material then separating into two masses around which new membranes were formed (1848, 1849). It was generally believed, however, that the origin of nuclei by division was of rare occurrence, and that ordinarily the nucleus dissolved just before cell-division, two new ones forming *de novo* in the daughter cells. Von Mohl (1851), who in the main agreed with Hofmeister, wrote as follows: "The second mode of origin of a nucleus, by division of a nucleus already existing in the parent-cell, seems to be much rarer than the new production of them . . ." And again, ". . . it is possible that this process [nuclear division] prevails very widely, since . . . we know very little yet respecting the origin of nuclei. Nägeli thinks that the process is quite similar to that in cell-division, the membrane of the nucleus forming a partition, and the two portions separating in the form of two distinct cells."

It was not until many years later, in connection with researches upon syngamy and embryogeny, that the behavior of the nucleus in cell-division became known in detail, and its probable significance pointed out. In 1879 Eduard Strasburger (1844–1912) announced definitely that *nuclei arise only from preëxisting nuclei.* W. Flemming was led to the same conclusion by his studies on animal cells, and expressed it in the dictum "*omnis nucleus e nucleo*" (1882*a*).

Interesting consequences followed from the extension of the Cell Theory by von Siebold and others to the Protozoa. The protozoan was found usually to be a uninucleate individual not unlike one of the cells of a larger animal or plant. It was therefore concluded that Protozoa are primitive one-celled organisms that in the course of evolution somehow aggregated to form a cell republic, the multicellular organism; and this was further taken to mean that the protozoan is to be homologized with a single cell of the multicellular body. This conception of the Protozoa and the phylogeny of multicellular organisms has been justly criticized by many biologists, who hold that if multicellular animals have evolved from Protozoa it has been by developing internal cellular structure rather than by colonial aggregation, and that the protozoan is therefore homologous with the entire multicellular individual (see Dobell, 1911*a*). Reference will again be made to this in Chapter III.

**The Protoplasm Doctrine.**—The Cell Theory and all of its corollaries were placed in a new light with the development of a more adequate conception of the significance of protoplasm. A number of early investigators had seen protoplasm and had been impressed by certain of its activities. As early as 1772 Corti, and a few years later Fontana (1781), saw the rotation of the "sap" in the Characeæ and other plants. After being long forgotten, these phenomena were rediscovered by L. C. Treviranus (1811) and G. B. Amici (1819). The cell to its discoverers meant nothing more than a wall surrounding a cavity; they spoke only in the vaguest terms of the "juices" present in cellular structures. The founders of the Cell Theory held a position but little in advance of this; they observed the cell contents but regarded them as of relatively slight importance.

Felix Dujardin (1801–1860) in 1835 described the "sarcode" of the lower animals as a substance having the properties of life. Von Mohl had seen a similar substance in plant cells, and in 1846, as noted above, he called it "Schleim," or "Protoplasma," the latter term having been used shortly before by Purkinje in a somewhat different sense. Nägeli and A. Payen (1795–1871) in 1846 recognized the importance of protoplasm as the vehicle of the vital activity of the cell; and Alexander Braun (1805–1877) in 1850 pointed out that swarm spores, which are cells, consist of naked protoplasm. An important point was reached when Payen (1846) and Ferdinand Cohn (1850) concluded that the "sarcode" of the animal and the "protoplasm" of the plant are essentially similar substances. In the words of Cohn:

> The protoplasm of the botanist, and the contractile substance and sarcode of the zoölogist, must be, if not identical, yet in a high degree analogous substances. Hence, from this point of view, the difference between animals and plants consists in this; that, in the latter, the contractile substance, as a primordial utricle, is enclosed within an inert cellulose membrane, which permits it only to exhibit an internal motion, expressed by the phenomena of rotation and circulation, while, in the former, it is not so enclosed. The protoplasm in the form of the primordial utricle is, as it were, the animal element in the plant, but which is imprisoned, and only becomes free in the animal; or, to strip off the metaphor which obscures simple thought, the energy of organic vitality which is manifest in movement is especially exhibited by a nitrogenous contractile substance, which in plants is limited and fettered by an inert membrane, in animals not so.

Protoplasm was now studied more intensively than ever. H. A. de Bary (1831–1888), working on myxomycetes and other plant forms, and Max Schultze (1825–1874), investigating animal cells, demonstrated the correctness of Cohn's view. The work of Schultze (1861) was especially important in that it firmly established the Protoplasm Doctrine, namely, that *the uniis of organization are masses of protoplasm*, and that *this substance is, in general, similar in all living organisms.* Schultze described the cell as "a mass of protoplasm containing a nucleus, both nucleus and protoplasm arising through the division of the corresponding elements of a preëxisting cell." The cell wall, upon which the early workers had focussed their attention, turned out to be of secondary importance. The cell was thus seen to be primarily the organized protoplasmic mass, to which Hanstein in 1880 applied the convenient term *protoplast.*

Extensive studies on the physical nature of protoplasm were soon undertaken. Brücke (1861), who was one of the first to lay emphasis on the fact that protoplasm is an organized substance, looked upon it as a contractile, semi-solid material through which there streams a fluid carrying granules. Similar to this was the idea of Cienkowski (1863), who believed he saw in the protoplasm of myxomycetes two fluids, one of them hyaline and only semi-fluid (the "ground substance"), and the other a more limpid fluid with granules suspended in it. De Bary (1859, 1864), on the other hand, regarded protoplasm as a single semi-fluid substance, contractile throughout, but showing many local differences due to varying water content.

More prominent were the structural theories associated with the names of Klein, Flemming, Altman, and Bütschli, and known respectively as the "reticular," "fibrillar," "granular," and "alveolar" theories. The reticular theory, which was formulated by Fromman (1865, 1875, 1884), was developed especially by Klein (1878–1879) and supported by van Beneden, Carnoy, Leydig, and others. These workers saw in protoplasm a reticulum or fine network of a rather solid substance (*spongioplasm*), which held a fluid and granules in its meshes.

The fibrillar, or filar, theory announced by Velten (1873, 1876), as a result of his observations on *Tradescantia* and other forms, stated that protoplasm is composed of fine fibrils, which, though often branched, do not form a continuous network. This idea was developed mainly by Flemming (1882), who called the substance of the fibrils *mitome* and the fluid bathing it *paramitome*. Some observers asserted that the fibrils were in reality minute canals filled with a liquid, the granules seen by others being merely sections of these canals. To the followers of the reticular and fibrillar theories the fluid held between the fibers was known variously as *ground substance*, *enchylema* (Hanstein, 1880), *hyaloplasm* (Hanstein), *paramitome*, and *interfilar substance*. The granules were known generally as *microsomes* (Hanstein).

According to the granular theory, protoplasm is a compound of innumerable minute granules which alone form the essential active basis for the phenomena exhibited; the observed fibrillar and alveolar structures are of secondary importance. For Altmann (1886, etc.), who was the most prominent exponent of the theory, the granules were actual elementary living units or "bioblasts," the liquid containing them being a non-living hyaloplasm. The cell was therefore looked upon not as a unit, but as an assemblage of bioblasts, "like bacteria in a zoöglœa," and the bioblasts were believed to arise only by division of others of their kind (*omne granulum e granulo!*).

The alveolar theory, also known as the emulsion, or foam theory, was elaborated principally by Bütschli (1892, etc.), and is of special interest in view of certain present-day notions of protoplasmic structure. According to Bütschli, protoplasm consists of minute droplets (averaging $1\mu$ in diameter) of a liquid "alveolar substance" (enchylema) suspended in another continuous liquid "interalveolar substance." The structure is, therefore, that of an extremely fine emulsion, and the appearances described by other workers are due to optical effects encountered in examining the minute alveolar structure. Bütschli supported his theory by making artificial emulsions with soaps and oils which showed amœboid movement and other striking resemblances to living protoplasm.

Later researches, to which reference will be made in Chapter II, have shown that it is in the hyaline "ground substance" that fundamental structure is to be sought, and that the appearances observed by the above pioneers do not have the significance originally attributed to them.

Von Mohl as early as 1837 held that the plastid is a protoplasmic body. The classic researches of Nägeli (1858, 1863) on plastids and starch grains laid the foundation for our knowledge of these bodies, which was greatly extended in later years by A. Meyer (1881, 1883, etc.) and A. F. W. Schimper (1880, etc.) (see Chapter V).

It would be difficult to overestimate the value, both practical and theoretical, of the Protoplasm Doctrine, for its establishment has not only led to knowledge by which the conditions of life have been materially improved, but has also been an important factor in assisting man to a modern, rational outlook on organic nature, in which he has learned to include himself. It is not too much to say that the identification of protoplasm as the material substratum of the life processes was one of the most significant events of the nineteenth century. The doctrine was furnished with a popular expression by Huxley in his well-known essay, *The Physical Basis of Life* (1868).

**The Organismal Theory.**—The conception of the cell had by this time developed into something quite different from what it had been in the minds of the founders of the Cell Theory. The cell was now recognized as a protoplasmic unit, and the ideas of these men concerning the origin of cells had been overthrown. Future researches were to show more clearly the rôle of cells in connection with development and inheritance, and certain limits were to be set to the conception of the cell as a unit of function and organization. To Schleiden and Schwann the multicellular plant or animal appeared as little more than a cell aggregate, the cells being the primary individualities; the organism was looked upon as something completely dependent upon their varied activities for all its phenomena. "The cause of nutrition and growth," said Schwann, "resides not in the organism as a whole, but in the separate elementary parts—the cells." This elementalistic conception of the organism as an aggregate of independent vital units governing the activities of the whole dominated biology for many years, notwithstanding its severe criticism by Sachs, de Bary, and many other later writers who pointed out that, owing to the high degree of physiological differentiation among the various tissues and organs, the cell cannot be regarded merely as an independent unit, but as an integral part of a higher individual organization, and that as such the exercise of its functions must be governed to a considerable extent by the organism as a whole (Wager).

That it is thus the living system as a whole, and not the individual cell, that is the "primary agent of organization" was definitely maintained by a number of biologists, who, unable to accept the Cell Theory, developed and supported the Organismal Theory.[1] In this connection may be mentioned the names of de Bary (1862), Sachs (1882), Rauber

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[1] This theory has been more widely known as the Plasma Theory, Tissue Theory, or Plasmodial Theory. See the recent works of Ritter (1919) and Rohde (1923).

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(1883), Heitzmann (1883), Hertwig (1884), Whitman (1893), Sedgwick (1894), Heidenhain (1902, 1907), Schlater (1911), Dobell (1911), Gurwitsch (1913), Ritter (1919), and Rohde (1885 . . . 1923).

According to this theory, evidence for which is to be cited in Chapter III, the multicellular plant or animal is not a colony or republic of elementary cell individuals, but rather a more or less continuous mass of protoplasm (plasmodium) which has become incompletely subdivided into subordinate centers of action, the cells, during the course of ontogenesis; cells are a result rather than the cause of development and differentiation. In the words of de Bary, "*die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen.*" The phylogenetic corollary of this theory is that multicellular organisms have evolved not by an aggregation of many individuals, but rather by the growth, differentiation, and septation of one, *i.e.*, by just such a process as is observable in the ontogeny.

If, now, we consider Lamarck's repeated statements to the effect that cellular tissue is the matrix in which organs are gradually formed as a result of the influence of internal and external influences, we recognize the interesting fact that it was the Organismal Theory more nearly than the Cell Theory that was foreshadowed in the mind of the great Frenchman. We have already alluded to the slow progress made by the Organismal Theory during the period of dominance of the Cell Theory, and to the increasing recognition which is being given it at the present day.

A number of special discoveries which further prepared the way for modern cytology will now be briefly reviewed.

**Syngamy and Embryogeny.**—*In Plants.*—Although it was known to the ancients that there is in plants something analogous to the sexual reproduction seen in animals, ideas of the organs and processes involved were very vague. Like Grew and others in the seventeenth century, the botanists of antiquity were aware of the fact that the pollen in some way influences the development of the ovary into a fruit with seeds. Definite proof that the stamens are the male organs (to speak somewhat loosely) was furnished in a well-known experiment by R. J. Camerarius (1691). But in spite of the excellent work of J. G. Koelreuter (1761), C. K. Sprengel (1793), and K. F. Gaertner (1849), all of whom proved the correctness of this conclusion, the idea of sexuality in plants was vigorously combated in certain quarters for many years.

An important step in advance was made when G. B. Amici (1830) followed the growth of the pollen tube from the pollen grain on the stigma down to the ovule. Schleiden (1837) and Schacht (1850, 1858) took up the study and made a curious misinterpretation. They regarded the ovule as merely a place of incubation for the end of the pollen tube, which they supposed to enter the ovule and enlarge to form the embryo directly. The work of Amici (1842), Tulasne (1849), and others showed the falsity of this notion, but an acrimonious discussion raged about the subject for a number of years, Schleiden (1842, 1844) using the most vigorous language in support of his position. After W. Hofmeister (1849) had followed the process with his characteristic thoroughness there could remain no doubt concerning the error of Schleiden and Schacht. Hofmeister clearly demonstrated that the embryo arises, as Amici contended, not from the end of the pollen tube, but from an egg contained in the ovule, the egg being stimulated to development by the pollen tube. He was wrong, however, in supposing that the tube did not open, but that a fertilizing substance diffused through its wall.

It was in the algæ that the union of the sperm cell with the egg cell (syngamy) was first seen in the case of plants. In 1853 Thuret saw spermatozoids attach themselves to the egg of *Fucus*, and in 1854 he showed that they are necessary to its development. The actual entrance of the spermatozoid into the egg was first observed in 1856 by Nathanael Pringsheim (1824–1894) in *Œdogonium*. The fusion of the parental nuclei was seen by Strasburger (1877) in *Spirogyra*, but he thought they thereupon dissolved. This error was corrected shortly afterward by Schmitz (1879*b*), who was thus the first to show clearly that the central feature of the sexual process in plants is the union of two parental nuclei to form the primary nucleus of the new individual. The demonstration of such a nuclear fusion in a number of algæ and fungi soon followed (see Tischler, 1921–1922, p. 462).

The fusion of the gametic nuclei in bryophytes and pteridophytes was first seen by Kruch (1890) in *Riella*, and by Campbell (1888) in *Pilularia*. That the same process occurs in syngamy in the seed plants was demonstrated by Strasburger, who in 1884 described the union of the egg nucleus with a nucleus brought in by the pollen tube. In 1898 and 1899 S. Nawaschin and L. Guignard completed the story by describing "double fertilization," wherein one male nucleus unites with the egg nucleus, and a second with the two polar nuclei to form the primary endosperm nucleus. The subsequent work of Strasburger and others on the gymnosperms and angiosperms greatly cleared up the whole matter of syngamy and embryogeny in these plants.

*In Animals.*—It is probable that the spermatozoön was first seen in 1677 by Ludwig Hamm, a pupil of Leeuwenhoek. The credit for the discovery, however, is usually given to Leeuwenhoek, since it was he who brought the matter to the attention of the Royal Society and pursued such studies further. He asserted that the spermatozoa must penetrate into the egg, but it was thought at the time and for many years afterward that they were parasitic animalcules in the spermatic liquid; hence the name "spermatozoa."

Although L. Spallanzani (1786) is usually said to have shown by his filtration experiment that the spermatozoön is the fertilizing element, it is pointed out by Lillie (1916) that Spallanzani did not draw the correct conclusion; he even denied that the spermatozoön is the active element, holding rather that the fertilizing power lies in the spermatic liquid. It was Prevost and Dumas who corrected this mistake and demonstrated the true rôle of the spermatozoön (1824). The spermatozoön was later shown by Schweigger-Seidel (1865) and La Valette St. George (1865) to be a complete cell with its nucleus and cytoplasm, as von Kölliker had maintained. That Schwann (1839) had been right in regarding the egg as a cell was shown by Gegenbaur in 1861. The polar bodies formed at the time the egg matures are said to have been first seen by Carus (1824). Bütschli (1875) showed them to be formed in connection with the division of the egg nucleus, and Giard (1877) and Mark (1881) interpreted them as abortive eggs.

The penetration of the spermatozoön into the egg was not actually seen until Newport (1854) observed it in the case of the frog. In 1875 O. Hertwig (1849–1922) announced the important discovery that the two nuclei seen fusing in the fertilized egg are furnished by the egg and the spermatozoön—by the two parents. The rôle of the nucleus in syngamy was thus demonstrated in animals only shortly before it was in plants, and it is interesting to note that the first complete description of the union of the germ cells in animals was given by H. Fol in the same year (1879) that Schmitz described clearly the process in plants. It was now evident that syngamy in both kingdoms consists in the union of two gametes which are ordinarily single cells, one from each parent (in diœcious forms), and that *the central feature of the process is the union of two gamete nuclei, the new individual therefore deriving a portion of its nuclear substance from each parent.*

Although the cleavage of the fertilized animal egg to form the embryo had been seen many years previously, it was first definitely described by Prevost and Dumas in 1824 for the frog. At that time neither the egg nor the products of its division were known to be cells. The true meaning of cleavage was elucidated by M. Barry, who held that the blastomeres are cells and that their division is preceded by the division of their nuclei, and by a number of later writers, including A. von Kölliker, Whitman, and Rabl, who traced in detail the long series of changes undergone by the multiplying embryonic cells as the various tissues and organs are differentiated. Embryogeny was thus shown to involve the division and differentiation of cells, the fertilized egg initiating a series of divisions giving rise to all the cells of the body, and to the germ cells. It was now possible to describe the life cycle in terms of cell successions; and since the egg is the descendant of the egg of the previous generation, it became evident that there has been an uninterrupted series of cell-divisions from the remote past down to the organisms in existence today. The statement of this conception, without, however, any necessary emphasis on cells rather than protoplasm itself, is known as the Law of Genetic Continuity. In the words of Locy (1915):

> The conception that there is unbroken continuity of germinal substance between all living organisms, and that the egg and the sperm are endowed with an inherited organization of great complexity, has become the basis for all current theories of heredity and development. So much is involved in this conception that . . . it has been designated (Whitman) "the central fact of modern biology." The first clear expression of it is found in Virchow's *Cellular Pathology*, published in 1858. It was not, however, until the period of Balfour, and through the work of Fol, van Beneden (chromosomes, 1883) Boveri, Hertwig, and others, that the great importance of this conception began to be appreciated, and came to be woven into the fundamental ideas of development.

**Mitosis and Meiosis.**—It has been shown that cells were believed by the founders of the Cell Theory to arise *de novo* from a mother liquor, or "cytoblastema," a misconception removed by later investigations in which it was shown beyond question that cells arise in general by the division of preëxisting cells. By several early observers the nucleus was seen to have a more or less prominent part in the process, its division preceding that of the cell, but

> . . . it was not until 1873 that the way was opened for a better understanding of the matter. In this year the discoveries of Anton Schneider, quickly followed by others in the same direction by Bütschli, Fol, Strasburger, van Beneden, Flemming, and Hertwig, showed cell-division to be a far more elaborate process than had been supposed, and to involve a complicated transformation of the nucleus to which Schleicher (1878) afterward gave the name *karyokinesis*. It soon appeared, however, that this mode of division was not of universal occurrence; and that cell-division is of two widely different types, which van Beneden (1876) distinguished as *fragmentation*, corresponding nearly to the simple process described by Remak, and *division*, involving the more complicated process of karyokinesis. Three years later Flemming (1879) proposed to substitute for these terms *direct* and *indirect* division, which are still used. Still later (1882*a*) the same author suggested the terms *mitosis* (indirect or karyokinetic division) and *amitosis* (direct or akinetic division), which have rapidly made their way into general use, though the earlier terms are often employed. Modern research has demonstrated the fact that amitosis, or direct division, regarded by Remak and his followers as of universal occurrence, is in reality a rare and exceptional process; . . . it is certain that in all the higher and in many of the lower forms of life, indirect division or mitosis is the typical mode of cell-division (Wilson, 1900, pp. 64–65).

The chromosomes, though they appeared in the figures of A. Schneider (1873), were first adequately described by Strasburger in 1875; and Waldeyer (1888) gave them their name. The longitudinal splitting of the chromosomes was discovered by Flemming in 1882, and shortly thereafter (1884) van Beneden and Heuser showed in animals and plants respectively that the daughter halves of each divided chromosome pass to opposite poles in mitosis. Drawings of the achromatic figure were published by Kowalevsky (1871) and Fol (1873), but Bütschli (1875) was the first to describe it in detail.

The discovery of meiosis was made by van Beneden, who in 1883 announced that the nuclei of the egg and spermatozoön of *Ascaris* each contain one-half the number of chromosomes found in the body cells. Although van Beneden and other early workers believed that the change in number was brought about by the simple casting out of half the chromosomes during the growth of the germ cells, it was soon found that this view was incorrect, and that "*reduction is effected by a rearrangement and redistribution of the nuclear substance* without loss of any of its essential constituents" (Wilson, 1900, p. 233).

In plants the discovery of meiosis came somewhat later. Strasburger in 1888 showed that in angiosperms the number of chromosomes in the egg and male nuclei is fixed by a reduction occurring in the megasporocyte and microsporocyte respectively. This was at once confirmed by Guignard (1889, 1891). E. Overton (1893) found that the female gametophyte cells in the cycad, *Ceratozamia*, have half the number of chromosomes present in the cells of the sporophyte. He further suggested that meiosis probably occurs in the sporocytes in mosses and ferns. In the liverwort, *Pallavicinia*, Farmer (1894) found the gametophyte cells to have four chromosomes and the sporophyte cells eight. That Overton's theory of meiosis in the sporocytes of bryophytes and pteridophytes was correct was demonstrated by Strasburger (1894), who postulated the occurrence of a periodic reduction in the number of chromosomes in all organisms reproducing sexually.

The further development of our knowledge in this and other departments of cytology will be followed in some detail in subsequent chapters.

As Wilson (1900, p. 6) points out, the many facts brought to light in the early days of cytology were of the greatest significance in connection with the Theory of Evolution and the problem of heredity, though for many years this was only vaguely perceived. Darwin, aside from his Hypothesis of Pangenesis, scarcely mentioned the theories of the cell; and not until many years later was the cell investigated with reference to these matters. Researches on the origin of the germ cells, nuclear division, and fertilization, which brought cytological research and the study of evolution into intimate association, began shortly after 1870 with the works of Schneider, Auerbach, Fol, Bütschli, O. Hertwig, C. Bernard, van Beneden, Strasburger, and Flemming; and these were followed by the noteworthy achievements of Boveri, Driesch, Herbst, Morgan, Loeb, and others. These men laid the foundations for the work which has followed; and their researches, greatly aided by the development of new refinements in microtechnique, ushered in modern cytology. A powerful stimulus to investigation was given when the zoölogists Hertwig, von Kölliker, and Weismann, and the botanist Strasburger, concluded independently and almost simultaneously (1884–1885) that the nucleus is the vehicle of heredity, an idea which Haeckel had put forward as a speculation in 1866. The announcement of this conception led to an even more intensive study of the nucleus and of its rôle in heredity, a study which is now in progress, and which, more than any other one thing, can be said to characterize the work of our modern period.

**The Twentieth Century.**—The year 1900 marks the beginning of a new era in cytology, for reasons which may be stated in the words of Wilson (1924, pp. 8–9):

> This era of cell research coincides with the new era in genetics that opened in 1900 with the rediscovery of the Mendelian phenomena of heredity by de Vries, Correns, and Czermak. This discovery was the outcome of purely genetic experiments on hybrids; but almost at the moment of its announcement, by a remarkable coincidence, cytologists had independently arrived at a point where the cytological basis of the phenomena could be clearly recognized. Rückert eight years earlier (1892) had briefly suggested a conjugation and disjunction of corresponding paternal and maternal chromosomes in meiosis and an exchange of material between them ("amphimixis of the chromosomes"), thus to a certain extent foreshadowing the modern explanation of the Mendelian segregation and of recombination by "crossing-over." Montgomery (1901), without knowledge of Mendel's fundamental law of segregation, brought together almost all of the essential data for its explanation, though he did not bring them into specific relation with the genetic phenomena. He pointed out the constant size differences of the chromosomes; emphasized the presence in the diploid groups of paternal and maternal homologues in pairs, and accepted the conjugation of these homologues in synapsis, and their disjunction in the reduction division. Boveri, in his remarkable paper on multipolar mitosis (1902), demonstrated experimentally the determinative action of the chromosomes in development and proved their qualitative differences in this respect. A possible connection between the Mendelian disjunction and the reduction division was suggested nearly at the same time by several observers, including Strasburger, Correns, Guyer, and Cannon. It was, however, Sutton (1902, 1903) who first clearly set forth in all its significance the cytological explanation of the Mendelian phenomena that is offered by the behavior of the chromosomes, and thus initiated the remarkable movement in this direction that followed.

Particularly noteworthy also is the modern renewal of the investigation of protoplasm, its inclusions, and its differentiations in the living state, a type of study which has been greatly promoted by the conception of protoplasm as a colloidal system. Not only is this resulting in the removal of many misconceptions growing out of the too exclusive use of fixed material, and the finding of partial explanations for a variety of puzzling cytological phenomena, but it is bringing cytology into a profitable association with physiology and physical chemistry, just as the study of chromosomes has allied it with genetics. No tendency of the present is more significant for the future of cytology and encouraging to the investigator than the formation of such alliances, for only through them is there much hope of coming nearer to a solution of the complex problems presented by the living organism.

# CHAPTER II

# PROTOPLASM

Huxley, in his famous essay of 1868, very aptly termed protoplasm "the physical basis of life." With a realization of the full significance of this phrase comes a conviction that protoplasm is the most interesting and important substance which can occupy the attention, for nowhere else in nature, so far as known, is life to be found.

In spite of the enormous amount of work which has been done upon protoplasm during a period of many years, our knowledge of its constitution and behavior must still be regarded as very superficial. Some have inclined to the view that a given kind of protoplasm is a single complex chemical compound, but at present it seems more probable that it represents a somewhat looser combination of substances, many of which are themselves very elaborate in composition. It furthermore seems probable that these substances differ from those found elsewhere not so much in their fundamental chemical nature as in the degree of their complexity, and especially in their mutual organization. Protoplasm is made up of proteins, fats, salts, water, carbohydrates, and other compounds, but it is not a mere mixture of these materials: it is an intricately *organized system* of substances of many types; and only by virtue of this specific physicochemical organization does it serve as the material substratum for those peculiar orderly activities characterizing the organism, namely, synthetic metabolism, irritability, reproduction, and adaptive response. Living protoplasm should always be thought of as a system in dynamic equilibrium; it is continuously maintaining itself through a balance of constructive and destructive processes. The "ability to transform environmental material into its own specifically organized and active substance is the distinctive criterion of living as distinguished from non-living matter" (R. S. Lillie, 1923).

**Chemical Nature of Protoplasm.**[1]—Protoplasm has repeatedly been subjected to chemical analysis. For this purpose the plasmodia of myxomycetes and the spermatozoa of fish have been most frequently employed, the former because of the large mass of relatively undifferentiated protoplasm easily available, and the latter because it affords a means of obtain-ing nuclear material in a nearly pure state. One of the most recent analyses of this kind is that of Lepeschkin (1923), who used the plasmodium of *Fuligo varians* (*Æthalium septicum*), the same species analyzed many years earlier by Reinke and Rodewald (1881). The results of Lepeschkin's analysis are as follows:

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[1] See on this subject Zimmermann (1896), Hammarsten (1909), Zacharias (1910), Czapek (1913, 1915, 1920), Wells (1914), Bayliss (1915), Mathews (1916, 1924), Palladin (1923), Meyer (1920), Robertson (1920), Moore (1921), R. W. Thatcher (1921), Walter (1921), Pratje (1920), Tischler (1921–1922, Chap. 2), Lundegårdh (1922, Pt. I, Chap. 11, B), Grafe (1922, Chap. 4), Onslow (1923), Trier (1924).

Water, 82.6 per cent by weight.
Dried matter, 17.4 per cent, in turn made up as follows:

A. Water-soluble organic materials, chiefly in vacuoles: amino acids, purin bases, asparagin, etc., 24.3 per cent; monosaccharides, 14.2 per cent; albuminous bodies, 2.2 per cent.

B. Insoluble in water, forming chiefly the ground mass of protoplasm:

| | Per Cent | | Per Cent |
|---|---|---|---|
| Nucleoproteids | 32.3 | Phytosterin | 3.2 |
| Free nucleic acids | 2.5 | Phosphatids | 1.3 |
| Globulin | 0.5 | Other organic matter | 3.5 |
| Lipoproteid | 4.8 | Mineral matter | 4.4 |
| Neutral fat | 6.8 | | |

The protein matter of protoplasm exists in relative complex forms. "The chief mass of the protein substances of the cells does not consist of proteids in the ordinary sense, but consists of more complex phosphorized bodies . . ." (Hammarsten). Such "phosphorized bodies" are the nucleo-proteins, which are "probably the most important constituents of the cell, both in quantity and in relation to cell activity" (Wells). A long series of chemical investigations beginning with the pioneer work of Miescher, Hoppe-Seyler, Reinke, Kossel, and Lilienfeld have shown that these nucleo-proteins are essentially combinations of nucleic acid with proteins.

The nucleus, as a rule, contains little or no uncombined carbohydrate, fat, or salt, but is characterized rather by the abundance of a nucleo-protein called *nuclein*, isolated in 1871 by Miescher, who gave it the formula $C_{22}H_{49}N_9P_3O_{22}$. It was shown by Altmann (1889) that nuclein, like the other nucleo-proteins, could be split into two substances: nucleic acid and a form of albumin (protein), the two existing in chemical combination like an ordinary salt; indeed, it is doubtful if nuclein should be regarded as a chemical individual (Czapek, Meyer). "Chromatin" appears to be such a combination of nucleic acid with a protein base. Nucleic acid, which is itself a combination of phosphoric acid and certain bases, seems to be very much the same in all types of protoplasm. So far there have been found only two general forms, differing chiefly in the carbohydrate constitution of the molecule: in one form it is a pentose and in the other a hexose. The former is known to occur in yeast, wheat, and certain animals, while the latter has been found in thymus and lymph glands, blood corpuscles, and spermatozoa. The strong affinity of nucleic acid for organic bases is responsible for the staining reactions of chromatin: a fixed and stained chromosome is a salt of nucleic acid with a basic dye. The basic constituent of living chromatin may be a very complex protein, a simpler and more basic histon (blood, thymus, echinoderm sperm), or a still simpler and more strongly basic protamine (fish sperm). Thus chromatin has been described as "a conjugated phosphoprotein group with a nucleic acid group, the latter group being a complex of phosphoric acid and a nuclein base" (Glaser, 1916).

The following scheme will help to make clear the relationships of these substances:

- Nucleo-proteins<br>Nuclein<br>("Chromatin")
  - Nucleic acid
    - Phosphoric acid
    - Pentoses or hexoses
      - Purin bases
      - Pyrimidins
      - etc.
  - Protein base: protamine, histon, or other protein

In the cytoplasm, in contrast to the nucleus, the proportion of protein constituents is relatively high. The cytoplasm probably has no true nuclein, but it is rich in nucleo-albumins, albumins, globulins, and peptones, which, unlike nuclein, contain little or no phosphorus. As a result its reaction is alkaline, in contrast to the acidity of the nucleus. According to Hammarsten (1909), "the globulins and albumins are to be considered as nutritive materials for the cell or as destructive products in the chemical transformation of the protoplasm." Globules of volutin, a nucleic acid compound often present in the cytoplasm, are looked upon as a reserve material for the nucleus, since they fail to form in a phosphorus-free nutrient solution (Reichenow, 1909; van Herwerden, 1917; Doflein, 1918).

The fatty components of protoplasm comprise both ordinary fats and lipoids (fat-like bodies not decomposed by alkalis). Among the latter lecithin and cholesterol are of great importance, particularly in animals.

The carbohydrates found in protoplasm are chiefly pentoses (plants) and hexoses (animals), which are, as a rule, combined with proteins and with lipoids. Glycogen exists free in many tissues and serves as a source of energy. The important rôle played by pentoses and pentosans in the activity of the plant cell has been strongly emphasized by Spoehr (1917, 1919) and MacDougal (1920); in fact, these authors speak of protoplasm as "an intermeshed pentosan-protein colloid."

Inorganic salts are present in considerable variety, as shown by the presence of the following elements in the ash of *Fuligo* protoplasm: chlorine, sulphur, phosphorus, potassium, magnesium, sodium, calcium, and iron.

The amount of water in protoplasm varies greatly under different conditions, but usually it is present in large proportions. It makes up from 85 to 95 per cent of the weight of actively streaming protoplasm such as is seen in *Elodea* and *Tradescantia*, and in actively functioning cells it rarely drops below 70 per cent. In dry spores, however, it may be reduced to 10 or 15 per cent, the protoplasm then becoming very viscous. The percentage differs constantly in different parts of a cell; nucleus, cytoplasm, and plastids, though all are composed primarily of protoplasm, contain very different amounts of water.

No single substance is of greater significance in the life of the organism than water. In the words of Henderson (1913):

> . . . the physiologist has found that water is invariably the principal constituent of living organisms. Water is ingested in greater amounts than all other substances combined, and it is no less the chief excretion. It is the vehicle of the principal foods and excretion products, for most of these are dissolved as they enter or leave the body [across the wall of the intestine and across the epithelia of kidneys, lungs, and sweat glands]. Indeed, as clearer ideas of the physico-chemical organization of protoplasm have developed it has become evident that the organism itself is essentially an aqueous solution in which are spread out colloidal substances of great complexity [Bechhold, 1912]. As a result of these conditions there is hardly a physiological process in which water is not of fundamental importance.

It is by no means solely by virtue of its great solvent power that water is so effective in promoting chemical interaction. Its exceptional ionizing power is especially noteworthy in this connection, while its high surface tension has a notable influence on reactions involving adsorption. There is also evidence that water is necessary to that most fundamental of vital processes, oxidation. The importance of these and other characteristics of water are discussed at length by Henderson (1913) in an inquiry into the biological significance of the properties of water.

The general significance of the results of analyses of protoplasm by chemical methods should be considered for a moment. A. Meyer (1920) has objected to the idea that such analyses as that of *Fuligo* really show the composition of living substance, for the reason that all the ergastic materials (non-living reserves and by-products) are included in the analysis. Furthermore, in such a delicately balanced system as protoplasm the analytical methods employed must cause a number of reactions which cannot be followed, with the resulting formation of compounds not present in the living condition. Later on, in reviewing Meyer's theory of protoplasmic structure, his reason for insisting so strongly on these points will be evident. That there is a certain amount of justification for these objections must be admitted, but it still remains true that chemical analyses give us much valuable information concerning the types of substances present in protoplasm and the relative proportions in which they occur. Such information is obviously prerequisite to any understanding of protoplasmic reactions.

The chief point to be borne in mind is that chemical analysis does not reveal what may be the most significant characteristic of protoplasm, namely, its peculiar organization. Just as in the case of any other operating system, such as a watch, the activities of protoplasm can be understood only if the structural relations of the materials composing it are known. The close dependence of the essential synthetic chemical reactions of protoplasm upon an essential type of structure present only during life has recently been admirably discussed by R. S. Lillie (1923, 1924).

**Physical Nature of Protoplasm.**[1]—Allusion has already been made to the notable advances made in our knowledge of protoplasm as a result of the renewed study of living material. Certain workers, notably Barber (1911, 1914), Kite (1913), Chambers (1914, 1915, 1917, 1918), Seifriz (1918, 1920), and C. V. Taylor (1920), have developed a technique whereby they have been able to dissect, inject, and otherwise operate upon living cells under the high powers of the microscope, thus opening a most promising field for investigation. Many of the facts cited in the following pages have been ascertained through the use of such methods.

Under the microscope living protoplasm appears to the eye as a colorless, optically homogeneous fluid, called *hyaloplasm*, in which there are usually imbedded granules and globules of varying size, shape, and number. It is commonly observed to be in a state of active streaming, notably in the vacuolate cells of plants. In the leaf cells of *Elodea*, for instance, the protoplasm is in almost continuous rotation, while the stamen hairs of *Tradescantia* afford a beautiful example of a more complex type of circulation. Various theories, involving electricity, contractility, surface tension, imbibition, and other phenomena have been propounded to account for such protoplasmic movement (see Meyer, 1921). Notwithstanding its own high water content, healthy protoplasm is usually if not always, non-miscible with water.

Noteworthy among the further general physical characteristics of living protoplasm are its elasticity and viscosity. These are properties which it is difficult to estimate quantitatively. Much has been learned about them through the use of microdissection apparatus, the centrifuge, and the Brownian movement of suspended granules; but Freundlich and Seifriz (1923) and Seifriz (1924*b*) have greatly increased the accuracy with which they can be measured by the ingenious use of electromagnets and inserted nickel particles. The viscosity of a great many types of protoplasm has now been studied, and it has been shown that the consistency varies greatly in different tissues, in different portions or organs of a cell, and at different stages of cell-division and differentiation. In general, it seems that animal protoplasm is on the average more viscous than that of plants. In nerve cells and non-dividing epithelial cells no Brownian movement is visible, even with dark-field illumination, but in plant cells, as well as in eggs and tissue-culture cells of animals, it may be readily observed (see Chambers, 1924). Seifriz (1924*a*) states that the viscosity of protoplasm is on the average about that of glycerine, and seldom below that of machine oil. The effects of a variety of reagents on protoplasmic viscosity have been ascertained by Heilbrunn (1920*c*, 1924), Jacobs (1922), Weber (1922, 1923), Scarth (1924), and others. The viscosity changes which occur in different regions of the cell during meiosis, syngamy, and cleavage have been studied with interesting results by Heilbrunn (1915, 1921) and Chambers (1919). Reference will be made to these in a later chapter.

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[1] See Chambers (1924), Lundegårdh (1922, Pt. I, Chap. 11; Pt. II, Chaps. 1–3), Meyer (1921), Schaeffer (1920), Harper (1919), Wilson (1923). For accounts of the new methods of microdissection and microinjection, see Barber (1914), Chambers (1918, 1921*a*, 1922*a*, 1924), C. V. Taylor (1920), Seifriz (1924*b*).

As already stated, protoplasm nearly always contains visible globules and other particles. These represent vacuolar material, chondriosomes, and more or less transitory nutritive substances of various types. Some cells show no such elements, or only chondriosomes, but this condition is exceptional. The smallest of the other visible granules, the "microsomes," are almost universally present, according to Chambers (1917, 1924). In the echinoderm egg there are, in addition, many larger "macrosomes" (called "alveolar spheres" by Wilson, 1899), which measure 3 or 4$\mu$ in diameter and seem to represent nutritive matter. Other bodies, such as fat and oil globules, are also present. All of these may be so abundant that the ground substance or hyaloplasm is practically invisible. Likewise, in plants especially, minute sap vacuoles may be so numerous that the protoplasm has an alveolar appearance. Fibrillar differentiations may further complicate the picture. It will be readily recognized that the optical appearance of a given sample of protoplasm depends very largely upon the kinds of inclusions present, their size and arrangement, and the degree to which they are crowded together (*cf.* Fig. 2).

A fact which is both striking and very significant is that protoplasm may be deprived of all these visible differentiations without losing the power of carrying on its characteristic activities. Hyaline pseudopodia amputated from granular amœbæ are irritable and move in the typical amœboid manner. Centrifuged sea urchin eggs can be cut into two portions, one with all the visible granules (except oil globules) and the other with none, after which both portions may be inseminated and undergo cleavage (see Chambers, 1924). This means that the visible elements, although they should be regarded as a part of the living system to the degree in which they are active in protoplasmic reactions (see p. 50), are not an essential part of that system; and that "it is in the apparently structureless hyaloplasm that the real problem of cytoplasmic organization lies" (Wilson, 1923). It is, therefore, primarily with the hyaloplasm that the following section on the colloidal state is concerned.

It is now somewhat easier to evaluate the early structural theories mentioned in the historical sketch. What their proponents saw was not the fundamental structure of protoplasm, but secondary structures arising as the result of the formation of differentiation products in the hyaloplasm. Thus Bütschli's alveoles were innumerable minute masses of vacuolar substances; any distinction between large vacuoles, alveoles and ultramicroscopic colloidal masses of the same material is more or less arbitrary, though the physico-chemical properties of the system may be expected to vary with the degree of subdivision. It does not appear strange that so many theories should have been propounded, now that it has been shown that all the supposed fundamental types of structure may occur in the same cell at different stages. Protoplasm shows no single universal type of visible structure, and such visible structure as it does show, though of much importance, is not ultimate.

**Protoplasm as a Colloidal System.**—No problem in biology is of more importance than that of the ultimate structure of the hyaline ground substance of protoplasm. It is here that cytology has received a notable contribution from the field of physical chemistry in the form of facts and hypotheses concerning the colloidal state of matter.[1]

*The Colloidal State.*—A substance is said to be in the colloidal state when it is sufficiently finely divided or dispersed. Adopting this flexible definition, it may be said that the student of colloids has to deal with bubbles, drops, grains, filaments, and films, because in each of these cases at least one dimension of the structure in question in small (Bancroft). The substance is, of course, enveloped in some other medium (gas, liquid, or solid), the two together constituting what may be termed a colloidal system. The dispersed substance is known as the internal phase, and the enveloping medium as the external phase, or medium of dispersion. Each of the physically homogeneous constituents, or *phases,* may be chemically complex; an aqueous phase, for example, may contain salts and other compounds in solution. The different chemical substances, including the solvent, which make up a phase, are called *components.* Furthermore, more than two phases may be present; there may be "polyphase systems," but it will be sufficient for our purpose to deal only with those involving two phases.

Colloids differ widely in general properties according to the liquid, solid, or gaseous nature of the two phases. It will be of service to cite examples:

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[1] See Bancroft (1921), Bayliss (1915, 1923), Bechhold (1919), Czapek (1911*b*), Hatschek (1916), Lundegårdh (1922, Pt. I, Chap. 11), Meyer (1920, Chap. 4), Robertson (1920) and Lepeschkin (1924). The student will find the works of Bancroft and Hatschek particularly useful.

Liquid in liquid: mayonnaise
Solid in liquid: muddy water
Gas in liquid: foam
Liquid in solid: jelly
Solid in solid: true ruby glass
Gas in solid: bread
Liquid in gas: fog
Solid in gas: smoke

The size of the colloidal particles (or the thickness of the filaments and films) ranges from that of bodies visible to the naked eye down to those approaching molecules in minuteness. Although it is possible to treat a true solution formally as the end term of a series of suspensions, Bancroft stresses the point that with a given pair of substances it may be impossible to form such a continuous series, for the reason that below a certain size the particles may be soluble, reprecipitating in a coarser form. As a rule, therefore, the particles are molecular complexes. Colloidal solutions are often classified as "suspensoids," in which the suspended matter is solid, and "emulsoids," in which it is supposedly liquid. It is chiefly the emulsoids that must be carefully considered in discussing protoplasm. Typically these are uncrystallizable, considerably more viscous than water, readily coagulable, only slightly or not at all osmotic, and poor electrical conductors. In all of these features they differ markedly from true molecular solutions.

If the suspended particles are much less than $0.2\mu$ in diameter they cannot be seen with the ordinary microscope; but in many cases their presence may still be detected with the ultramicroscope, under which they appear as bright points against a dark field, or by the Tyndall phenomenon. In case they happen to have the same optical properties as the medium of dispersion, however, these methods will not reveal them. Wolfgang Ostwald (1917) gives the following comparative table of diameters:

| | |
|---|---|
| Red blood corpuscle | $7{,}500\text{m}\mu (= 7.5\mu)$ |
| *Staphylococcus* | 800 |
| Particles in fine mastic suspension | 500–1,000 |
| Casein particles in milk | 130–170 |
| Colloidal gold particles | 2–15 |
| Molecule of soluble starch | 5 |
| Molecule of haemoglobin | 2.5 |
| Molecule of grape sugar | 0.7 |
| Molecule of hydrogen | 0.1 |

The peculiar properties and behavior of colloidal systems are further due in large measure to the enormous extent of the reacting surface (interface) between the constituent phases. It can readily be calculated that a cube of matter 1 centimeter in each dimension and exposing 6 square centimeters of surface would expose 60 square centimeters if cut into 1-millimeter cubes, 6 square meters if cut into $1\mu$ cubes, and 6,000 square meters if cut into $1\text{m}\mu$ cubes.

Closer attention should be given to *emulsions*, because of their prominence in the literature pertaining to protoplasm. Two immiscible liquids, such as water and oil, may be beaten up together with the resulting formation of a two-phase emulsion. Ordinarily the suspended droplets tend to run together if the mixture be allowed to stand, the two phases finally separating out completely. In order that the emulsion shall be stable it is usually necessary to add an "emulsifying agent," or third substance which will pass into the interface between the phases and form a thin viscous film about each of the suspended droplets, preventing their coalescence. Mayonnaise dressing, for example, is an emulsion of oil in an aqueous medium (vinegar), with egg as an emulsifier. Such interfacial films also have an important effect upon the electrical properties of the system. Stability in many cases is brought about by adsorbed ions; all of the droplets may be similarly charged and so repel one another. Here the addition of an electrolyte neutralizing these charges will cause precipitation.

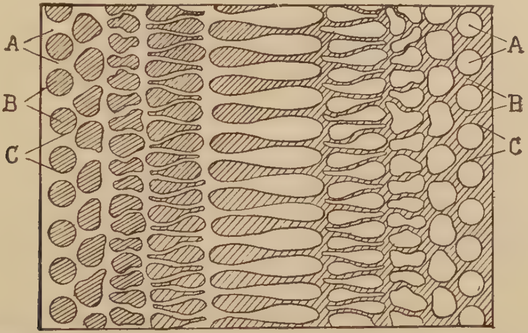

FIG. 1.—Diagram illustrating phase reversal in a colloidal emulsion. *A*, aqueous phase. *B*, oil or other non-aqueous phase. *C*, interfacial film formed by emulsifying agent. (*After Clowes*, 1916.)

The character of the emulsion depends largely upon the nature of the emulsifying agent employed, because of the unlike effects which different substances have upon surface tension at the interface. If, for example, sodium or potassium oleate be used in an oil-water system, the result is an emulsion of oil in water; whereas calcium or magnesium oleate brings about an emulsion of water in oil. Thus by employing both sodium and calcium salts, varying their ratio, the important change known as *phase reversal* may be secured at will in either direction (Fig. 1). At a certain critical ratio there is a very delicate balance between the two conditions; and it is a biologically significant fact that Clowes found this ratio to be about the same as that in which the two classes of salts occur in sea water.

The relative volumes of the phases are also important in determining the physical character of emulsions and foams. Water with a few minute air bubbles in suspension has essentially the properties of water alone, but when the volume of the air greatly exceeds that of the water, as it does in a light foam, the consistency of the whole is very different. Similarly, the suspended droplets in an emulsion may be well separated and free to move upon one another; or they may be very closely packed, or agglomerated in larger masses, giving the system a much firmer consistency. The former type of emulsion may appear granular or alveolar, whereas the closely packed type has a honeycomb structure appearing in section as a reticulum (Fig. 2). Furthermore, the suspended droplets may at times partially run together, both phases then being continuous, and the whole having the form of a spongework, or *interlacing system.* A good example of an interlacing system of gas and solid may be seen in sponge cake or bread.

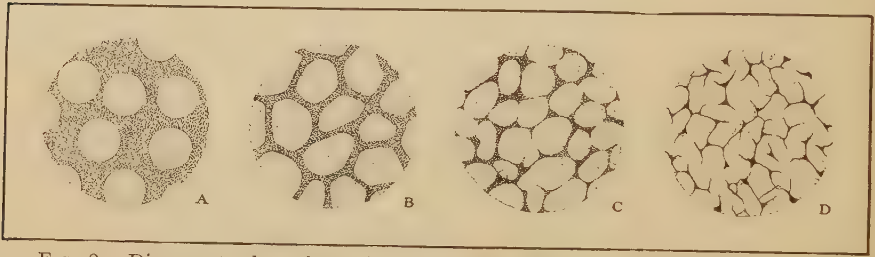

Fig. 2.—Diagram to show the various appearances observable in a two-phase colloidal emulsion. *A*, suspended droplets well separated, giving an alveolar appearance. *B*, droplets crowded, giving continuous phase a reticular appearance. *C*, *D*, aspects due to a proportionally smaller amount of the originally continuous phase and a coalescence of the droplets, both phases becoming continuous.

Colloidal solutions with separate mobile particles are generally referred to as *sols*, and those with a more gelatinous or semi-solid consistency as *gels*, but these terms have not been uniformly used, and all possible intermediate conditions exist. A colloidal system may be made to pass from the gel to the sol state (peptization) or from sol to gel (gelation; pectization). In some cases (heated gelatin) such an alteration is reversible, but in others (coagulation[1] of egg albumen) it is not. Gels include coagula (gelatinous precipitates) and jellies, but the structure of neither type is well known. Gelation has been said to involve phase reversal in certain cases, the denser phase becoming external; but the evidence now at hand indicates rather that an agglomeration or a partial coalescence of the suspended droplets occurs, with the resulting formation of a reticulum or a spongework of threads. Meyer (1913), for example, found that starch-water jellies have a net structure made up of globules, and other investigators have interpreted certain inorganic gels also as essentially three-dimensional networks (see Bancroft, 1921; Seifriz, 1924*a*).

With these general facts concerning colloidal structure in mind, the consideration of protoplasm may be resumed.

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[1] Coagulation is here used to denote a gelation involving a radical structural alteration which is normally irreversible.

*The Colloidal Nature of Protoplasm.*—The work of the past few years has made it abundantly clear that protoplasm is essentially a colloidal system. This is manifest in its general physical properties. Its viscosity, surface tension phenomena, and high electrical resistance are like those of other known colloids. So also are its powers of adsorption, which lie at the basis of many of its reactions and certain staining processes. Its semi-permeable properties are typically those of colloidal systems; a semi-permeable region is probably present wherever protoplasm comes in contact with other substances, such as water. Protoplasm shows most strikingly its colloidal character in the alterations of physical state, involving imperfectly understood structural changes, which it undergoes as a result of variations in external conditions and internal reactions. Local temporary alterations of this nature are known to accompany a number of important life processes. Protoplasm, like many organic and inorganic colloids, is irreversibly coagulated by high temperatures and a variety of chemical substances. The "fixation" of protoplasm by the reagents employed in cytological technique is primarily a coagulation phenomenon; and in the act of coagulation a substance, especially one as complex as protoplasm, undergoes a decided alteration in physical structure. Although such fixing fluids preserve very well the general structure of cells, the effect of coagulation should always be borne in mind in interpreting finer details, and in evaluating the results of special studies on the ultimate structure of protoplasm. The work of A. Fischer (1899), who treated ordinary proteins with cytological fixing reagents and so produced artifacts similar to alveoles, reticula, and granules, should make one cautious in drawing conclusions regarding protoplasmic structure from fixed material. It should be understood that the only trustworthy observations are those which are made at least in part on livng material.

Since the properties to which reference has been made above are exhibited primarily by the hyaloplasm, one "cannot resist the evidence that the appearance of a simple, homogeneous colloidal substance offered by the hyaloplasm is deceptive; that it is in reality a complex, heterogeneous, or polyphase system" (Wilson, 1923).

Protoplasm is colloidal, but the question of the particular type or types of colloidal structure it possesses is one to which no definite answer can yet be given. The most widely prevalent theory is that it has essentially the emulsion type of structure, with discontinuous phases of lipoids, proteins, and other liquid and solid substances suspended in an aqueous medium. It has been thought by some that high electrical resistance indicates a discontinuity of the water phase (M. Fischer, 1923), some non-conducting material constituting the medium of dispersion. The suddenness of many permeability changes has been thought to favor the view that protoplasm has an emulsion structure, at least in plasma membranes (Clowes, 1916) (see p. 40). R. S. Lillie (1923) sees further evidence in a variety of phenomena, including the autolytic action of injured cells, wherein enzyme and substrate are allowed to interact by the breakdown of films normally separating them. The nature of the emulsifying agent is unknown. There is a general tendency to regard the films separating the phases as lipoid (soapy?) in nature (Clowes, Lillie), although other emulsifiers are more abundant in protoplasm (Seifriz, 1923). Clowes based his conclusions largely on his observation of the effects of various salts on the behavior of oil-water emulsions.

The view that the colloidal constitution of protoplasm is primarily that of an emulsion has been brought into question by Seifriz (1924 *ab*). He points out that living protoplasm differs markedly from emulsions in its noticeable degree of elasticity, its power of imbibition, and its characteristic behavior in forming a granular irreversible coagulum at death. His interesting comparison of the behavior of protoplasm with that of certain inorganic colloidal solutions is summarized as follows:

> When a dividing echinoderm egg, in the metaphase of mitosis, is subjected to the pressure of the surface tension existing between a cover slip and a thin film of water, the entire mitotic figure, consisting of a highly viscous jelly cortex which encloses the dilute polar regions and the spindle, suddenly collapses, leaving not a vestige of the structural features of the preceding karyokinetic figure. This collapse is analogous to the sudden breakdown of certain inorganic gels, namely, of iron oxide, as described by Schalek and Szegvary, and of metallic cadmium, as described by Svedberg. In all three cases the sudden liquefaction is brought on by mechanical disturbance, in protoplasm by pressure, and in the two inorganic gels by stirring or shaking. These analogous phenomena tend to support the micellar hypothesis of the structure of gels, a structure in which the colloidal units are connected one to the other to form a three-dimensional network.

The common view that the process of reversible gelation is one of dehydration and hydration is discussed by Seifriz in the light of these results, and it is concluded that "viscosity changes in protoplasm, as in non-living inorganic jellies, are probably purely a matter of structural changes, of a reorientation of structural units whether micellæ or molecules, and are not due to, though they may be accompanied by, hydration or dehydration."

From the foregoing account it is not to be concluded that investigators insist that all protoplasm must have this or that particular type of colloidal structure. It is probable that the minute structure varies within wide limits in different tissues and in different regions of any differentiated mass of protoplasm. It may be that emulsions, interlacing systems, and molecular bridgeworks all actually exist, and pass one into the other according to general and local conditions. Only future research will permit an evaluation of the many conflicting views on this subject. The point to be borne in mind at present is that the structure in any event is indisputably colloidal, and that our attempts to explain protoplasmic behavior must be based on this fundamental fact. We shall proceed, then, with the general conception of protoplasm as a complex system of many substances dispersed in the form of granules, globules, filaments, networks, and plates, which thus expose an enormous area of reacting surface in proportion to their volume; and an extensive series of thin films in the interfaces between the continuous and dispersed phases, between the differentiated protoplasmic regions or organs, and around the mass as a whole. In addition there may be the partitions which make a cellular tissue.

Some of the activities of protoplasm which seem clearly to be conditioned by its polyphase, film-partitioned organization may now be briefly enumerated (see Bayliss, 1923; R. S. Lillie, 1923).

A great variety of chemical substances coëxist in protoplasm without interacting until certain conditions prevail, whereupon interaction occurs suddenly and extensively. This is thought to involve films separating the different phases of the system. Under appropriate circumstances the properties of these films are rapidly altered, allowing the substances on either side to interact, and the volume and the velocity of the reaction are due in large measure to the enormous area of reacting surface. The periodic character of certain processes involving oxidation and enzyme action is probably to be so explained. A particularly important case of the control of reactions through changes in colloidal films is seen in general and local alterations in the permeability of the plasma membrane bounding any unit mass of protoplasm, a matter to be discussed in the next section.

Such properties and behavior on the part of films separating various regions within a protoplasmic mass permit the localization of very diverse types of chemical activity within a small space, and the consequent differentiation of organs (*e.g.*, nuclei and plastids) in which these activities are then more efficiently carried on. Thus a given mass of protoplasm, such as a cell, may be said to have a "chemical organization" (F. Hofmeister, 1901). A more complete realization of the possibilities of such protoplasmic differentiation is seen in a multicellular tissue, which is essentially a mass of protoplasm pervaded by a series of semi-permeable membranes. Here there is a field for the fuller play of surface reactions, and the basis for a more complete organic differentiation (see Chapter III).

The effect of colloidal structure upon processes involving adsorption is noteworthy. Substances are typically more subject to chemical change when adsorbed at surfaces than when distributed uniformly in solution. Adsorption is frequently a necessary preliminary to chemical reaction (Bayliss). In protoplasm there exists an ideal structural basis for such "adsorption catalysis;" in fact, it seems that "the determination and control of chemical reactions by adsorption are universal in living protoplasm" (Lillie, 1923). It seems clear that a part of the catalytic activity of enzymes is due to their colloidal state. These facts may suggest why it is that certain reactions, such as rapid oxidation, ordinarily occurring only at high temperatures, may take place at very low temperatures in the organism.

Finally, in the film-partitioned structure of protoplasm there is the basis for electrical phenomena, a subject fully discussed by Lillie. Electric currents have been shown to accompany a variety of vital processes, and to have a fundamentally important bearing upon problems pertaining to the reception and conduction of stimuli, automatic or reflex activity, muscular contraction, the movement of plant parts, correlation, polarity, growth, and other biological phenomena. "They appear, in fact, to be as essential a feature of protoplasmic action as the consumption of oxygen or the evolution of $CO_2$."

**Ectoplasm and the Plasma Membrane.**—It has long been known that there is at the free surface of any mass of protoplasm a layer whose physical properties differ somewhat from those of the substance within the mass. In amœbæ and myxomycetes a layer of hyaline *ectoplasm* may easily be distinguished from the granular *endoplasm* within (Fig. 3). The ectoplasmic layer, or *ectoplast*, has the appearance of a region in which the granular elements have withdrawn from the hyaline ground substance (Pfeffer, 1890), though this may not be the proper explanation of its origin. Frequently the boundary between ectoplasm and endoplasm is not at all sharp, and it seems evident that the two may readily be converted into one another. In the Protista, as will be shown further on, the ectoplast is often very conspicuously differentiated, and may be accompanied by additional envelopes. In ordinary tissue cells special surface layers are usually not directly observable, and much difference of opinion exists with regard to their nature. The structural relations of the protoplasm and the surrounding cellulose wall of the plant cell are particularly difficult to determine (Chapter XI).

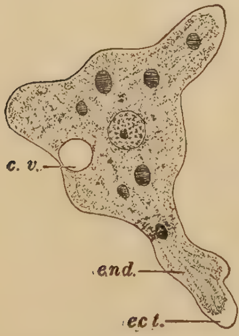

Fig. 3.—*Amœba*, showing ectoplasm, endoplasm, and contractile vacuole.

There is a large body of experimental evidence which indicates that a superficial *plasma membrane* is always present at the boundary of any protoplasmic mass, whether or not any special ectoplasmic layer may be distinguished. In case such a layer is present, the plasma membrane represents its outermost surface film. Much has been learned about the plasma membranes of amœbæ through observations on the behavior of particles adhering to it (Schaeffer, 1920) and by the use of microdissection apparatus (Kite, 1913; Chambers, 1917; Seifriz, 1918, 1921). In myxomycetes, for example, Seifriz finds that the outer membrane is distinctly more elastic and tenacious than the hyaline layer immediately beneath; although it is exceedingly thin it is a definite morphological structure, which may actually be removed after death with the dissecting needles. Moreover, it is capable of constant repair. Such a capacity to form a surface membrane and repair it after injury seems to be universally present in healthy protoplasm. The manner of its development is in many respects like that of the formation of surface films by other colloidal systems, although in the case of protoplasm certain metabolic syntheses seem to be involved. Lillie (1918, 1923) speaks of the plasma membrane as "a portion of the living protoplasm, characteristically modified in its structure and physical properties by surface conditions." Because of the very different surface conditions which prevail in the case of tissue cells, the differentiations can scarcely be expected to be wholly the same as in naked masses of protoplasm, but there is much evidence to show that in both cases specialized plasma membranes furnish a basis for the explanation of certain physiological facts.[1]

*Permeability.*—Since the ultimate structure of the plasma membrane lies beyond the reach of the microscope, the problem of its constitution must be approached through a study of its physiological behavior; in fact, the chief interest in structure here lies in its relation to the physiologically important property of permeability. Although hypotheses of other kinds have been put forward to account for the osmotic activities of cells, experimental data have practically demonstrated the general correctness of Pfeffer's (1890) theory that semi-permeable membranes (membranes permeable to solvent but not to solute) are primarily responsible for these phenomena. That the surface membrane has properties of impermeability not present in the endoplasm is interestingly shown by the fact that certain substances, eosin, for example, to which the membrane is impermeable will diffuse readily through the endoplasm if artificially injected through the membrane (Chambers, 1924). The permeability of a vacuolate cell is the algebraic sum of the permeabilities of all the regions traversed—outer plasma membrane, endoplasm, and vacuole membrane; but the result is due chiefly to the membranes. The membrane bounding the nucleus is another important semi-permeable region.

One of the most influential theories of the physico-chemical constitution of the plasma membrane has been that developed by E. Overton (1895, etc.) in a number of contributions. It is generally known as the lipoid theory.

> The grounds on which it is based are several, of which the following are the most important: first, the non-miscibility of protoplasm with water, which can plausibly be accounted for by the presence of a film of some sort of fatty material;

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[1] For discussions of surface membranes, see Schaeffer (1920), Bayliss (1921), Lundegårdh (1922), R. S. Lillie (1923), Chambers (1924), and Jacobs (1924).

second, the fact that lipoids are substances which have a high degree of "surface activity" and which might, therefore, reasonably be expected from the Principle of Gibbs to collect at free surfaces, automatically repairing injuries, etc.; and third, the almost perfect correlation which Overton found between the lipoid solubility of hundreds of organic compounds and the ease with which they enter cells (Jacobs, 1924).

It was therefore concluded that the membrane must consist very largely of the lipoids lecithin and cholesterol, which are known to occur widely in protoplasm. This theory, though very suggestive, was opposed by Ruhland (1909, 1912, 1915) and several other investigators, who called attention to a number of substances which are not absorbed according to the requirements of the theory, and to certain properties of lecithin which appear to diminish its importance. (Ruhland, it may be mentioned, has revived the ultra-filter theory suggested by Traube, namely, that the membrane acts as a molecular sieve.) But the fact remains that lipoids are undoubtedly an essential constituent of the plasma membrane. This conclusion has received support in the recent researches of Weis (1925), who finds that the many fine strands extending from the plasmolyzed protoplast to the wall in *Allium* cells react to reagents in the manner of lipoids; but he adds that an albuminous constituent seems to be present also. Other investigators also (Ramsden, 1904; Osterhout, 1911; Loeb, 1911; and others) have made it clear that proteins are very important in this connection. The tendency at present, therefore, is to look upon the plasma membrane as a layer made up chiefly of lipoids and proteins in some form of colloidal combination (the "mosaic theory" of Nathansohn).

The view that the plasma membrane has the structure of an emulsion is the one most commonly held. According to Czapek (1910, 1911, 1915) "protoplasm is a colloidal emulsion of lipoids in hydrocolloidal media, the latter containing proteins and mineral salts." Lepeschkin (1910, 1911) thought it probable that the lipoids form the continuous phase. Clowes (1916) made the interesting observation that the sodium-calcium ratio in sea water and animal body fluids is about the same as that at which oil-water emulsions undergo phase reversal, and advanced the view that similar reversals of lipoid and aqueous phases may account for the marked alterations in permeability shown by the plasma membrane. That changes other than phase reversal may be concerned in alterations of permeability also seems evident. Thus variations in the degree of colloidal dispersion may play a rôle in determining such alterations (Spaeth, 1916). If permeability is largely a matter of solubility in a continuous colloidal phase, the membrane should allow substances to pass much more rapidly when the suspended particles are far apart than when they are closely packed. Lloyd (1915) and Free (1918) suggest that, since colloids are known which "have two liquid phases which differ in composition only in the relative proportion of water and of the substance of the colloid" (Free), it is possible that alterations in permeability may be due to changes in the distribution of water between two such phases present in the plasma membrane. When water passes from the internal (suspended) to the external (continuous) phase, the droplets of the former would become very small; when the movement is in the opposite direction they would become very large and closely packed. As a result there should occur such changes in the physical nature of the membrane as would aid in interpreting the behavior of the latter toward substances entering or leaving the cell. It is held that such a hypothesis accounts more readily for gradual changes in permeability than does the inversion theory of Clowes, according to which the change might be expected to occur more suddenly. Both gradual and sudden alterations in permeability occur, and it is highly probable that they are brought about through structural changes of more than one type.

*Protista.*—The ectoplast shows its most elaborate structural differentiations in Protista, where it clearly has several functions—protective, motor, excretory, and sensory (see Minchin, 1912, Chap. V). In many forms there is a relatively tough outer envelope, or "pellicle," in addition to the more fluid hyaline ectoplasm. The origin and degree of development of this envelope, however, are not the same in all cases. Commonly, it seems to arise as a modification of the outer region of the ectoplast. In some amœbæ Chambers (1924) states that the hyaline ectoplasm is not visible, the granular protoplasm apparently lying directly against the pellicle. The "periplast" of flagellates also seems to represent the entire ectoplast modified. In still other forms the resistant envelope is formed indirectly by secretion.

Among the ectoplasmic structures with a motor function the simplest are the *pseudopodia;* in the larger ones there is a core of endoplasm (Fig. 3), but the more delicate "filose" ones consist entirely of ectoplasm (Fig. 4). Bayliss (1920) finds that minute suspended particles can be detected in hyaline pseudopodia by the use of dark-field illumination, their Brownain movement affording an index of the fluidity of the ectoplasm. The flagellum of *Euglena* was reported by Bütschli to have an elastic endoplasmic core with a contractile ectoplasmic sheath (Fig. 5, *A*), but the later figure of Dellinger (1909) represents it as composed of four twisted filaments ending within the animal as a system of branching rootlets (Fig. 5, *D*). In *Spirillum* such contractile filaments are separable, but in *Chromatium* they are firmly united (Metzner, 1920). *Cilia,* which are short and numerous and show rhythmic pulsation,[1] *cirri,* which are formed of tufts of cilia, *membranellæ,* representing fused rows of cilia, and *undulating membranes,* which are mainly sheet-like extensions of the ectoplasm

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[1] For discussions of the structure and mechanics of flagella and cilia, see Heidenhain (1911), Lundegårdh (1922), and Metzner (1920).

(Fig. 5, *B*), are all essentially ectoplasmic organs. In *Blepharisma* Chambers and Dawson find that when touched with a needle the undulating membrane breaks up into cilia, which may reunite. A further motor differentiation is seen in the minute contractile fibrils known as *myonemes*, which are analogous to a system of muscle fibers (Fig. 5, *C*). In ciliated forms they run beneath the rows of cilia. That the action of cilia in certain Protozoa is controlled by a distinct "neuromotor apparatus" has now been demonstrated (see p. 318).

Contractile or pulsating vacuoles, which exercise an excretory function, originate in the ectoplasm, although they may later lie much deeper. In certain cases definite actively protective organs, the *trichocysts*, are differentiated in the ectoplasm. A sensory function is performed by the "eyespot," which is sensitive to light, and also by the flagella and cilia, which are often receptors of tactile stimuli. The eyespot seems in some instances to be plastid-like in character, and will be discussed in Chapter V.

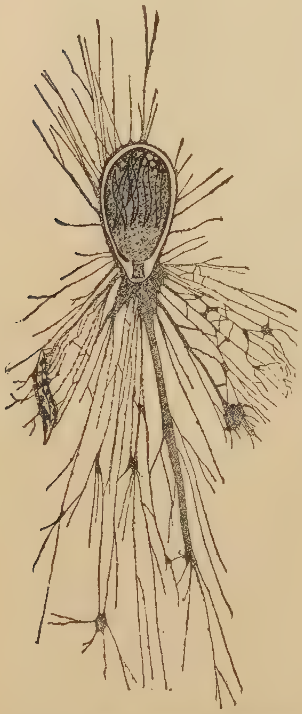

FIG. 4.—*Gromia oviformis*, showing filose-reticulate pseudopodia composed of ectoplasm. (*From Minchin, after Schultze.*)

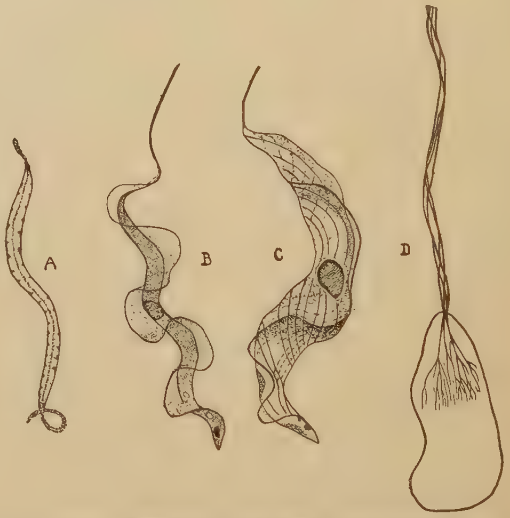

FIG. 5.—*A*, flagellum of *Euglena*, showing endoplasmic core and ectoplasmic sheath. (*After Bütschli.*) *B*, *Trypanosoma tincæ* with undulating membrane. (*After Minchin.*) *C*, *Trypanosoma percæ*, showing myonemes. (*After Minchin.*) *D*, flagellum of *Euglena*. (*After Dellinger.*)

**Vacuoles.**[1]—Although any fluid-filled cavity in protoplasm may be looked upon as a vacuole, the term is ordinarily used with reference to cavities containing the watery solution known as cell sap. Such cavities seem to be bounded by distinct membranes with semi-permeable properties similar to those of the external plasma membrane. Vacuoles are comparatively inconspicuous in animals, but in plants they appear to be almost universally present and clearly play a most important rôle in the metabolic processes. In plant meristems they are frequently numerous and very minute, but as the cells grow and differentiate they coalesce and grow enormously, often far exceeding in actual volume the protoplasm in which they took their origin (Fig. 11). The passive division of vacuoles has occasionally been observed (de Vries; Went; Küster, 1918*b*). The vacuolar system of a single cell, whether consisting of one or more vacuoles, is called the *vacuome* by Dangeard.

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[1] See Meyer (1920 Pt. VI, Chap. 6), Lundegårdh (1922, Pt. II, Chap. 8), and P. Dangeard (1923*a*).

The oldest and most prevalent view concerning the origin of vacuoles in plants is that they simply arise *de novo* in the protoplasm wherever water becomes abundant enough to form visible droplets (von Mohl, Nägeli, and many later writers). As a result of his study of meristems, de Vries (1885) advanced the theory that vacuoles do not arise *de novo*, but rather from individualized bodies which he called *tonoplasts.* As the tonoplast secretes cell sap within itself, it gradually enlarges and becomes the vacuolar membrane, which is still referred to as the tonoplast. Since the tonoplast bodies were supposed to multiply only by division, de Vries looked upon vacuoles as permanent constituents of protoplasm, like nuclei. This theory had the support of Went (1888).

Pfeffer (1890) undertook to test experimentally the power of protoplasm to form vacuole membranes anew. He introduced soluble granules of asparagin into the plasmodium of a myxomycete and found that membranes were formed about the resulting droplets. Although there is some question concerning the application of this fact to the problem of normal vacuole formation, Pfeffer concluded on the basis of this and other evidence that vacuoles do arise *de novo* in protoplasm, as von Mohl had held, and that the theory of de Vries is untenable. For many years thereafter the view of von Mohl and Pfeffer, with or without qualification, was generally accepted. Strasburger (1898), for instance, who regarded protoplasm as mostly alveolar in structure, accounted for the origin of vacuoles by the enlargement and coalescence of alveoles; and Meyer (1912, 1920) classed them as accumulations of ergastic fluid around which membranes are secondarily formed.

A new period in the study of vacuoles begins with the recent researches of P. A. Dangeard (1916, etc.), who has again advanced a theory, supported also by P. Dangeard (1922, 1923), that the vacuolar system (vacuome) is a permanent constituent of the cell. Treated with vital dyes (cresyl blue, neutral red, methylene blue) in meristematic plant tissue, the vacuome at first appears in the form of minute "metachromes;" these enlarge, absorb water, and develop into a system of anastomosing canals which finally become one or more large vacuoles without special membranes (Fig. 6, *a-d*). Such a system of "canaliculi" had been seen several years earlier in the root tips of plants by Bensley (1910), who, like Dangeard, found that they are not preserved by ordinary methods of fixation (Fig. 42). The Dangeards report further that in the maturing endosperm of *Ricinus* the vacuole, in which protein matter develops, passes through a reticular stage and breaks up into smaller vacuoles which become aleurone grains. At the time of germination the process is reversed: the grains become small vacuoles, which coalesce to form a network and finally a large vacuole (Fig. 6, *f-o*). Pollen grains also show a vacuome in the form of vacuoles, aleurone grains, or a reticulum. It is accordingly concluded that the vacuome is an autonomous system present in all plant cells in the form of minute metachromes, recognizable

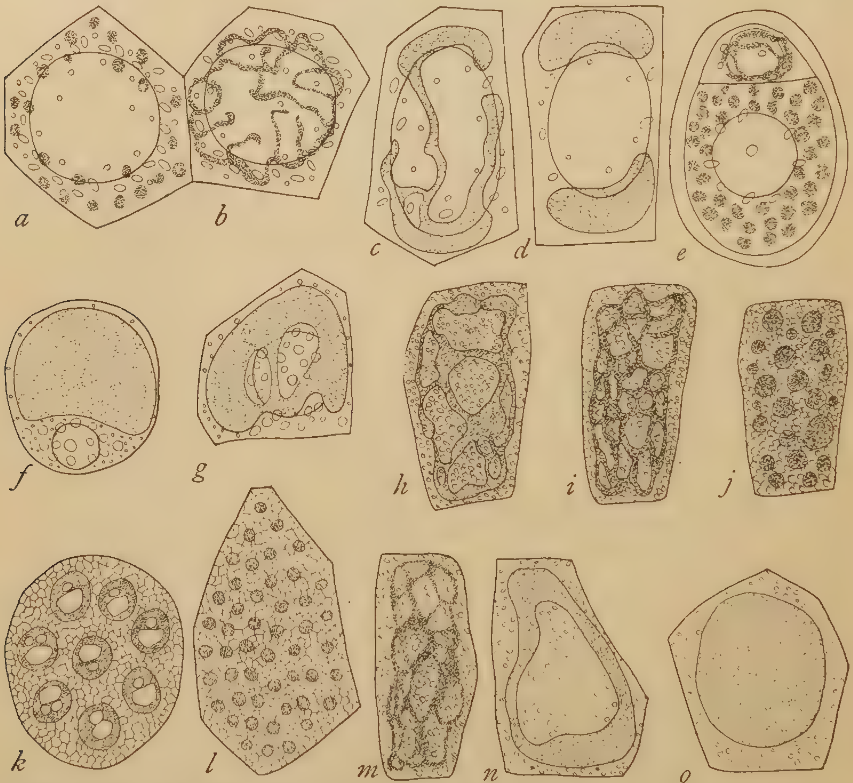

FIG. 6.—The behavior of the vacuole system in certain plant cells. *a–d*, cells in successive stages of development in the bud of *Abies*. *e*, pollen grain of *Cephalotaxus*. *f–j*, formation of aleurone grains from vacuole system in endosperm cells of *Ricinus*. *k*, deeply lying endosperm cell of *Ricinus*, with typical aleurone grains. *l–o*, peripheral cells of *Ricinus* endosperm, showing development of vacuole from simple type of aleurone grains during germination. (*After P. Dangeard*, 1923. The colors in the original figures are represented here by stippling.)

vacuolar material, or aleurone grains; and that by repeated division it is passed on from cell to cell and from generation to generation. Guilliermond (1920*h*, 1922*c*), who has observed that the vacuolar system of a new apical segment of a fungus hypha is formed by the extension of the system in the adjacent segment, shares the views of the Dangeards concerning the autonomous nature of the vacuome. He emphasizes the point that vacuoles should not be regarded as colloidal substances which absorb or give up water according to physical conditions. It seems clear in any event that it is the vacuolar material itself, rather than the cavity containing it, that is of significance.

The above observations of the Dangeards and Guilliermond are of special interest for two reasons. First, at the reticular stage the vacuolar system bears a most striking resemblance to the Golgi material of animal cells, so that a number of investigators have been inclined to view the two as homologous (see Chapter VII). Second, if future research should show that the development of vacuoles is under the influence of special bodies passed on from one generation to the next, and especially if it should be shown that vacuoles never arise *de novo*, a view which at present does not appear plausible, the geneticist would have a new basis for the explanation of certain peculiar cases of inheritance (Chapter XVIII).

Chemically, the cell sap consists of water with a variety of substances in molecular and colloidal solution (see Chapter VIII). According to P. Dangeard (1923*a*), its reactions with vital dyes indicate an alkaline condition in meristematic cells, a change to the neutral or acid state accompanying the appearance of certain phenolic compounds, such as tannin. As long as the sap is alkaline the vital dyes change color when absorbed ("metachromasis"), but when it becomes acid this no longer occurs. It is the hypothesis of P. A. Dangeard that this reaction and the semi-permeable character of vacuoles in general are due not to a limiting membrane, but to the presence of a fundamental vacuolar constituent, a protein known as *metachromatin*. This is ordinarily in solution, but may be precipitated out as "metachromatic corpuscles."[1] Guilliermond dissents from Dangeard's view that this protein is identical with the metachromatin of the fungi, and attributes the staining properties of vacuoles to phenolic compounds.

The osmotic properties of vacuoles are of much importance in maintaining the turgor necessary to the proper functioning of plant cells, and in determining the utilization or disposition of reserves and by-products. Vacuoles frequently play a distinct morphogenetic rôle. It is by their action, for example, that large masses of protoplasm are subdivided into spores in certain fungi (Chapter XI). They are also directly concerned in the development of the capillitium filaments in myxomycetes (Harper, 1914; Harper and Dodge, 1914).

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[1] In a more recent paper Dangeard (1925) applies the term "chromidium" to the colloidal solution in the vacuole, and speaks of metachromatic corpuscles as "endochromidia."

The contractile vacuoles of Protista and the swarm cells of certain algæ and phycomycetes have a distinct excretory function. C. V. Taylor (1923*a*) has made a study of the structure and behavior of the contractile vacuole in *Euplotes*, using the new methods of microdissection and microinjection. He finds that the primary contractile vacuole, which is accompanied by two adjacent series of smaller vacuoles, discharges its contents through a definitely localized but temporary ectoplasmic pore, whereupon it disappears completely. Its place is then taken by another formed by the union of secondary adjacent vacuoles (Fig. 7). These latter vacuoles arise in turn from still smaller ones, which seem either to be derived ultimately from vacuoles containing granules that dissolve, or to arise *de novo* as fluid centers causing the protoplasm to form a membrane through gelation. Taylor's results are thus of special interest in connection with the discussion of vacuoles of other types, since they show that relatively tough vacuole boundaries may arise by a gelation of the protoplasm, and later disappear completely by a return to the sol condition. The bearing of this fact on the supposed autonomy of ordinary vacuoles is obvious.

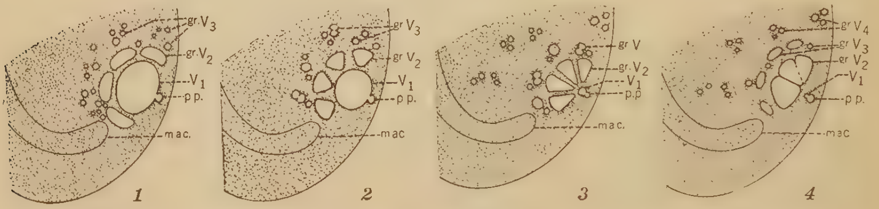

FIG. 7.—Discharge of the contractile vacuole ($V_1$) and the accompanying behavior of subsidiary groups of vacuoles (*gr.* $V_2$, *gr.* $V_3$) in *Euplotes*. *p.p.*, papilla pulsatoria. *mac.* macronucleus. (*After C. V. Taylor*, 1923.)

**Varieties of Protoplasm.**—From the foregoing résumé it is plain that protoplasm, because of the many combinations possible among constituents present in such great variety, is a substance which may exist in a vast number of different forms. When it is further recalled that many of the constituents exhibit singly the phenomenon of isomerism, this number is seen to be incalculable. For example, it was shown by Miescher that an albumin molecule with 40 carbon atoms could have about 1,000,000,000 isomers, and some albumins probably have more than 700 carbon atoms. Albumin, moreover, is only one of many complex substances present in protoplasm. Hence, the statement that all living cells are composed of the same substance, protoplasm, is true only in a general sense. Although they are made up of the same categories of substances existing in the same general type of organization—the hydrocolloidal state—the protoplasms of different organisms vary widely in the relative amounts of these leading constituents. For example, the lipoids are much more abundant in the protoplasm of animals than in that of plants, and the carbohydrate-protein ratio also shows notable differences in the two kingdoms. Qualitative differences are no less significant. The carbohydrates, which in plants are chiefly pentoses and in animals chiefly hexoses, may be cited. Analogous differences also exist between the smaller plant and animal groups, and with these differences in chemical constitution are associated many characteristic diversities in metabolic activity. Thus it is not simply with protoplasm but with protoplasms that the working biologist has to deal.

Special emphasis has been placed upon the relation of this great diversity in the constitution of protoplasms to the amazing variety observed among living organisms by Kossel, E. T. Reichert, and a number of other writers. Reichert and Brown (1909) have shown that each animal species examined has its own characteristic type of hæmoglobin, and that relationships may be indicated by degrees of similarity in the crystals of this substance. The same situation is found in the case of starch in plants (Reichert, 1913, 1919). That the specificity of organisms is probably primarily a matter of protein diversity is strongly indicated by the phenomena of immunology.[1] As Reichert states, the evidence seems to indicate that

> . . . in different organisms corresponding complex organic substances that constitute the supreme structural components of protoplasm and the major synthetic products of protoplasmic activity are not in any case absolutely identical in chemical constitution, and that each substance may exist in countless modifications, each modification being characteristic of the form of protoplasm, the organ, the individual, the sex, the species, and the genus.

**Protoplasm and Metaplasm.**—Because of the prominent place they occupy in cytological discussions, it will be well to outline several classifications of the substances composing organisms which certain writers have found useful.

J. Hanstein (1868):

1. *Protoplasm*—the living substance.
2. *Metaplasm*—non-living substances in or on protoplasm.[2]

M. Heidenhain (1902, 1907):

1. *Protoplasm*—the principal form of living substance.
2. *Metaplasm*—a less active form of living substance, formed by a process of differentiation in protoplasm in connection with special functions, and capable of growth, response to certain stimuli, and further differentiation. It is represented

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[1] See Reichert (1914) and R. S. Lillie (1923, Chap. 3 and literature there cited); also the discussion by Reed (1923).

[2] It was in this sense that "metaplasm" was used in the first edition of this book. In this edition it is used in Heidenhain's sense, and Meyer's term "ergastic substances" is used for non-living substances.

chiefly by the intercellular substance of animals; also by certain other structures, such as elastic and connective tissue fibrils.

3. Non-living substances.

E. Rohde (1908, 1914, 1923):

1. *Protoplasm*—the principal form of living substance.

2. *Metaplasm*—a less active form of living substance; essentially the same as Heidenhain's metaplasm, but including also contractile and nerve fibers, which Heidenhain regarded as protoplasmic. Metaplasm, according to Rohde, is formed not by cells but by a plasmodium, the cells being marked out by the differentiation of masses or sheets of metaplasm. It cannot again become protoplasm, and does not continue from generation to generation.

3. Non-living substances.

A. Meyer (1896, 1920):[1]

1. *Protoplasm*—the principal form of living substance.

2. *Alloplasm*—a less active form of living substance; essentially the same as the metaplasm of Heidenhain and Rohde. Cilia, flagella, and cytoplasmic fibrils are "alloplasmatic organs." Organs of this class arise by direct transformation of all or part of a protoplasmatic organ, usually the cytoplasm. They may dissolve, but do not become protoplasm again.

3. *Ergastic substances*—non-living substances arising anew in or on the protoplast; these correspond to the metaplasm of Hanstein. The intercellular substance, regarded as living by Heidenhain, is held to be ergastic by Meyer.

**Protoplasm and Life.**—Since the true significance of protoplasm was first recognized in the middle of the last century, many suggestions have been ventured regarding the nature of the relation existing between life and its physical basis. The modern conception of protoplasm as a living system was preceded by a number of speculative "micromeric theories," or "atomic theories of biology," according to which the principle of life was held to reside in ultimate vital particles.[2] Thus one reads of the "organic molecules" of Buffon, the "microzymes" of Béchamp, the "plastidules" of Haeckel, the "physiological units" of Spencer, the "bioblasts" of Altmann, the "plasomes" of Wiesner, the "inotagmata" of Engelmann, the "gemmules" of Darwin, the "pangens" of de Vries, the "biophores" of Weismann, and the "protomeres" of Heidenhain. Such fundamental particles were supposed to be for the most part of ultramicroscopic size, capable of growth and reproduction by division, and associated like members of a vast colony in protoplasm. They were compared by some to chemical molecules, but they were more generally regarded as molecular complexes; and many of them, notably those of Spencer, Darwin, de Vries, and Weismann, were postulated largely to account for the phenomena of heredity (see Chapter XXI).

One of the first investigators to insist strongly on the primary importance of the ultramicroscopic structure ("metastructure") of the hyaloplasm was Heidenhain, who criticized some of his predecessors for thinking that the essential structure of protoplasm must be visible. He pointed out the improbability of the supposition that significant structure ceases at the limit of microscopic vision (*cf.* Wilson, 1923), and followed Wiesner in developing a theory that the body represents a series ("biosystem") of parts of different rank ("histomeres"), the smallest and most fundamental of these being the "protomere."

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[1] Meyer used the adjectives "protoplasmatic" and "alloplasmatic," but we have substituted the corresponding nouns to facilitate comparisons with related theories.

[2] For summaries of these theories, see Delage (1903), Heidenhain (1907), Kellogg (1907), Meyer (1920).

A. Meyer (1896, 1920) also emphasized the fact that protoplasm is essentially an optically homogeneous watery colloidal solution, all visible structure being due to the presence of fluid or solid ergastic inclusions. But after the removal of these inclusions the hyaloplasm still contains in colloidal or molecular solution representatives of the same classes of materials (carbohydrates, salts, lipoids, proteins, etc.); since, Meyer said, such materials are ergastic in the visible form, they must also be regarded as ergastic when in solution. If, now, it were possible to remove both the visible ergastic structures and these invisible "ergastic organ-stuffs," there would remain the true living substance, which Meyer conceived as an association of water molecules and "vitules." It was to these vitules that the differences between protoplasm and other colloidal systems were attributed, whereas the ergastic substances were held chiefly responsible for the similarities, as well as for the results of all chemical analyses for protoplasm. The vitules were supposed to differ somewhat in nucleus, cytoplasm, and plastid, and to consist of smaller entities called "mions." Meyer's further speculations need not be discussed.

Reference should also be made to certain attempts to account for the activities of protoplasm on the basis of the chemical reactions of certain of its constituents, notably the proteins. It is not surprising that the peculiar properties of these compounds, which are certainly very significant, should have led to the belief that life is primarily a series of changes in special labile protein molecules, or "biogens" (Verworn). Adami (1908, 1918) has contended that life is "the function, or sum of functions, of a special order of molecules" which he calls "biophores" (not to be confused with the biophores of Weismann, which were molecular complexes), and which take the form of proteins when subjected to chemical analysis. The molecule of living matter (biophore) is one of "extraordinary complexity, and in a state of constant unsatisfaction, built up by linking on other simple molecules, and as constantly, in the performance of function, giving up or discharging into the surrounding medium these and other molecular complexes which it has elaborated" (1918, pp. 251–252). Accordingly, life is "a state of persistent and incomplete recurrent satisfaction and dissatisfaction of . . . certain proteidogenous molecules" (1908, Vol. I, p. 55). Mathews (1924) also writes concerning the relation of molecular condition to life. "Living matter contains molecules having a high content of energy and capable of passing to a more stable dead form in which they contain less energy." "It is the presence of the energy-rich forms which characterizes protoplasm" (pp. 25, 91).

The foregoing micromeric and chemical interpretations may now be briefly criticized.

Most modern biologists do not approve of attempts to assign the principle of life to any particular substance or structural unit in protoplasm, notwithstanding their appreciation of the service rendered by those who point out the suggestive properties of certain components, such as the proteins. The fundamental fallacy involved in much of the speculation on this subject lies in attributing the properties of a system to one or more of its constituent elements, and consequently in attempting to draw a sharp line between "living" and "lifeless" components. Sachs (1892, 1895) and many others have urged that the various elements should be referred to as active and passive rather than living and lifeless. It cannot be emphasized too strongly that protoplasm is a *living system* of components which of themselves are non-living—a system composed of all the substances that are participating in protoplasmic reactions at a given moment (*cf.* Wilson, 1923).

The various constituents of protoplasm share in all degrees in determining the activity of the system of which they are integral parts. It is probable that protoplasm always contains visible or invisible materials which might be removed without terminating the life processes. This does not prove, however, that these materials had no share in the processes while they were a part of the system, but shows only that the system which remains after their removal still has an organization permitting it to continue in the living state. It is an altered system, and operates in a somewhat altered manner. Furthermore, the same chemical compound may be active at one moment and relatively inactive at another, depending upon its physical state (*e.g.*, whether in solution or not) and the presence of other substances with which to react. It is not a certain chemical composition, but activity, that marks a substance as a part of the living system, for life is a process. These considerations enable one to understand why Meyer was compelled to resort to hypothetical vitules.

The removal of materials from protoplasm could obviously not be carried on indefinitely without depriving it of its characteristic powers; there is a certain minimal degree of complexity below which life as we know it is impossible. This fundamental system remaining after the supposed removal of all dispensable materials always comprises many classes of substances, some of which, notably water, carbon, and proteins, are probably essential in all forms of protoplasm because of their peculiar properties. But the fact that these forms of protoplasm are almost innumerable suggests that the components of the fundamental system must vary quantitatively, qualitatively, and in their type of structural organization within considerable limits. In any case it should be evident, in spite of the special importance of certain forms of matter, that it is not this or that component, but the organized system as a whole, which lives. Steel is not a time-keeping material, but it may be an especially important constituent of a time-keeping system, such as a watch. Proteins are not living compounds, but they are important constituents of living systems. The same may be said of the structural parts which these materials compose. Protoplasm, as Harper (1919) says, is a colloidal system in which special processes and functions have become localized and fixed in certain regions; and this in turn has resulted in the differentiation of organs (nuclei, plastids, etc.) possessing more or less permanence. Child (1915) remarks that theories postulating vital units only transfer the problems of life from the organism to something smaller; the fundamental problem of coördination is no nearer solution than before, and the whole question is placed outside the field of experimentation.

We may go a step further and point out that the organism, which is essentially a highly differentiated protoplasmic mechanism, is not to be sharply set apart from the environment. The two are so inseparably interlocked that they must be conceived as a single integrated system whose orderly operation is life.[1] Thus life is largely a relation or adjustment between the properties of the organism and those of the environment (Brooks, 1889), or, as Herbert Spencer put it, a "continuous adjustment of internal relations to external relations."

**Conclusion.**—As stated at the opening of the present chapter, it is with protoplasm that the phenomena of life, so far as known, are invariably associated. The complex behavior of the living organism can receive scientific explanation (*i.e.*, be fitted into an orderly scheme of antecedents and consequents), if at all, only on the basis of the constitution and properties of the materials composing protoplasm; the structural organization of protoplasm; the relation of the reactions of protoplasm to the environmental conditions; the chain of energy changes occurring in connection with all of the organism's activities; and the correlation of all these conditions and events. It is largely the effort to account for organization and regulatory correlation, and the consequent behavior of the complex organism as a versatile and consistent unit or individual, that has led to certain present-day vitalistic theories, as opposed to those which regard life as a phenomenon appearing in protoplasm solely by virtue of the peculiarly organized configuration or system of physicochemical conditions existing there.

Whatever the ultimate judgment of this matter shall be—for judgment at present would be premature—it can scarcely be denied that the working hypotheses which have thus far been most stimulating to research in biology, and most valuable in analyzing the data afforded by this research, are those which seek to formulate vital activity in terms of what the physicist calls matter and energy, and which hold life to be the manifestation not of a super-organic, non-perceptual entity, or even of a distinct perceptual but hypothetical vital energy, but rather that of the system of correlated interactions involving only energies of known kinds. The way should not be closed, however, against the possible appearance of new categories of energy in new systems. In the attempt to describe, or reduce to order, our perceptual experience of organic nature, achieved results would seem to justify the judicious use of hypotheses permitting one so far as possible to "describe the changes in organic phenomena by the same conceptual shorthand of notation as suffices to describe inorganic phenomena" (Pearson). Here one should guard against the common error of supposing that the action of any system is adequately described or explained by analyzing it into its component elements. The properties of a chemical compound are not those of its elements, but of the system which they constitute. Similarly, even if it be granted that the organism is ultimately a physico-chemical system, it is hardly sufficient to say that a biological process is explained when it has been decomposed into its physico-chemical components. That which is distinctively biological inheres not in the several components, but in their unique integration and the consequent peculiar action of the organized system as a whole. A true conception of the organism can be attained only when analysis into physico-chemical components is followed by resynthesis into a biological whole.[1] The need of non-mechanical principles in our ultimate biological theory can be properly estimated only after future investigation has greatly extended the scientific description (orderly formulation) of organic nature, and has shown with what degree of adequacy inorganic phenomena themselves are to be resumed in mechanical formulæ.

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[1] For discussions of this point, see Jennings (1924) and Sharp (1925).

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[1] See on this point J. A. Thomson (1920) and C. Lloyd Morgan (1923).

# CHAPTER III

## CELLS

Protoplasm is prevailingly organized in the form of cells. In the present chapter it will be seen that the concept of the cell is one for which it is scarcely possible to formulate a definition which will be sufficiently inclusive and at the same time precise enough to be useful. Cells differ widely in their structure, morphological rank, and mode of origin, but it is nevertheless useful to have before us the idea of a "typical" cell as a small mass of cytoplasm containing a nucleus and limited by a semipermeable membrane. This is obviously a crude description rather than an adequate definition, but it will serve our immediate purpose. The bodies of many minute plants and animals consist of but one such cell, whereas those of larger forms comprise large numbers of them; and there are other interesting types which fall in neither of these categories. Comparisons of such cases have led to many of our principal conceptions—and misconceptions—of the development and phylogeny of organisms. Since our underlying theory is that the cellular organization of plants and animals is a consequence of the growth and differentiation of protoplasm, it is from this angle that our subject may be approached.

**The Growth and Differentiation of Protoplasm.**—Apparently, one of the earliest and most important differentiations undergone by evolving living matter was the segregation of cytoplasm and nucleus. Certain nucleo-proteins with special functions depending on their peculiar properties are universally present in protoplasm, and in nearly all cases they are localized in distinct regions, forming what are known as nuclei. Nucleated protoplasm is the basis of further differentiation, and with it, therefore, our discussion may begin.

The fundamental importance of the capacity for *growth* is too obvious to require emphasis. The synthetic processes which result in the growth of the living mass involve an extensive interchange of materials between nucleus and cytoplasm, so that a certain proportion of nuclear and cytoplasmic substances (the "nucleoplasmic ratio") must be maintained if these processes are to continue. The part which any single spherical nucleus can play (its "sphere of influence") is strictly limited by the simple fact that its surface, through which the interchanges occur, does not increase at the same rate as does its volume. The further growth of the protoplasmic mass therefore requires a relative increase in the nuclear surface. This is sometimes accomplished by a change in the shape of the nucleus; but the almost universal method is by nuclear division, whereby the nuclear surface is increased without a corresponding change in volume. This permits further growth up to the point at which the critical ratio is again reached, whereupon the process is repeated.

The same principle is applicable to the relation between the protoplasmic mass and its environment. The size which a globular mass of protoplasm can attain through an increase in the actual amount of its substance is limited by a critical ratio between its volume and the amount of surface through which interaction with the external environment is carried on. The maintenance of the volume-surface ratio necessary to a proper metabolic equilibrium in the growing mass is secured in several ways. The mass may simply divide into two, thus increasing the surface without immediate increase in volume, and incidentally multiplying the number of individuals (Protozoa and Protophyta). A second method is by change of shape. This is well exemplified in cœnocytic plants, such as *Vaucheria* (Fig. 8, *V*), *Mucor*, and the myxomycetes, in which large masses of protoplasm expose an extensive surface by assuming a flat, spreading form (myxomycetes), or by developing filamentous branching bodies (cœnocytic algæ and phycomycetes). At the same time the nucleoplasmic ratio is maintained by repeated nuclear division, the numer-

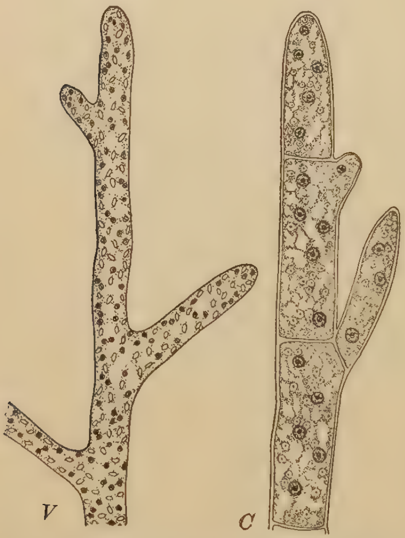

FIG. 8.—*V*, portion of cœnocytic body of *Vaucheria;* nuclei dark and plastids in outline. *C*, portion of semi-cœnocytic body of *Cladophora.*

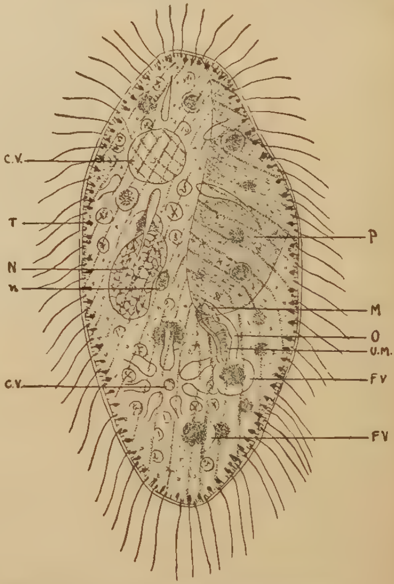

FIG. 9.—*Paramœcium caudatum.* *C.V.*, contractile vacuoles. *T*, trichocyst. *N*,*n*, mega- and micronuclei. *P*, peristomial groove. *M*, mouth. *O*, œsophagus, with undulating membrane, *U.M.* *F.V.*, food vacuoles. Semi-diagrammatic. (*After Lang.*)

ous nuclei being either relatively fixed in position (*Caulerpa*) or free to move about with the flowing cytoplasm (phycomycetes, myxomycetes).

Such cœnocytic bodies may be surprisingly elaborate, but the degree of complexity which they attain is nevertheless limited. The functional differentiation of regions in continuous large masses of protoplasm, which soon shows itself in visible structural differentiations, may be considerable; but the degree of differentiation reached by the higher classes of plants and animals seems to have been very largely conditioned by the development of diffusion-hindering partitions between the various centers of activity (nuclei) and functionally differentiating regions, the regions thus set apart then becoming more fully specialized than would have been possible in a continuous aqueous colloidal medium (see R. S. Lillie, 1923). The protoplasmic body thus attains a multicellular organization.

The formation of partitions[1] and the division of the nuclei show various degrees of correlation in different organisms. The two processes may be quite independent, in which case the compartments (cells) contain varying numbers of nuclei (*e.g.*, *Cladophora*, Fig. 8, *C*). In many cases, however, they are so intimately related that they are often thought of as one process, and the result is a regularly uninucleate condition of the cells. Here growth may appear to be a matter of cell multiplication, but a consideration of protoplasmic masses not showing such a correlation between nuclear division and cytoplasmic septation suggests that the regularly uninucleate cellular condition is the result of a specially refined mode of growth and differentiation. The great importance of this refinement in connection with the evolution of organisms is indicated by its prevalence. The more effective differentiation which such an organization makes possible permits, in turn, the fuller development of highly specialized tissues which serve to keep the various parts of the growing organism in correlation with one another (nervous system) and in proper relation with the environment (vascular and respiratory systems). Thus cell partitions not only extend the field of surface phenomena and condition a higher degree of organic specialization, but they also increase the range of body size attainable.

**Description of the Cell.**—The term *cell* was introduced by Robert Hooke and the other microscopists of the seventeenth century, who applied it to the small cavities in the honeycomb-like structure which they discovered in plant tissues. Today the term denotes primarily the protoplasmic "cell contents," to which, strangely enough, the early workers attached little importance. The term *protoplast*, proposed by Hanstein (1880), is more appropriate and is coming into more general use, but long usage and brevity have insured the permanence of the older term. The morphology of a "typical" or "ideal" cell will here be sketched in its barest outlines, by way of introduction to the detailed descriptions and discussions involving cells in the subsequent chapters.

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[1] By direct differentiation of membranes or by furrowing (see Chapter XI).

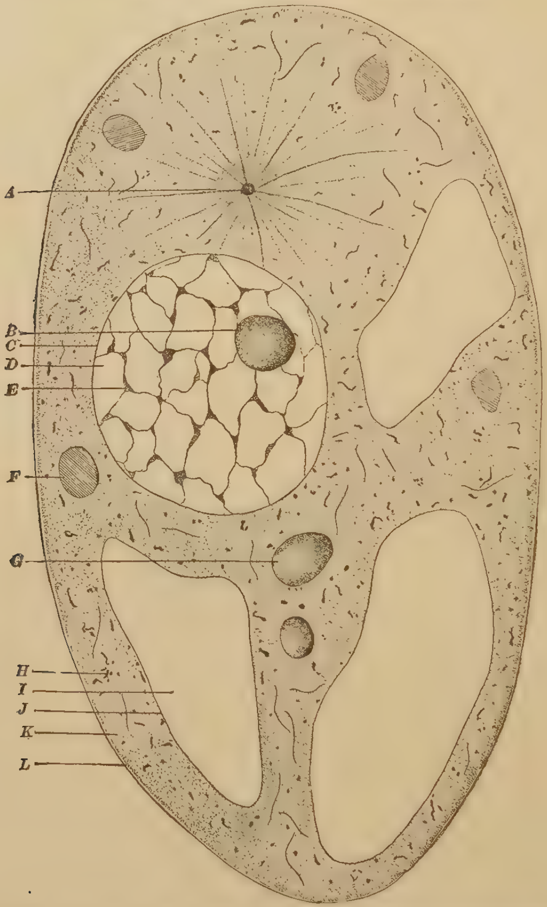

FIG. 10.—Diagram showing the more common differentiations which may occur in a cell. *A*, centrosome, composed of centriole and centrosphere, and surrounded by aster. *B*, nucleolus. *C*, nuclear membrane. *D*, karyolymph. *E*, chromatic reticulum of nucleus. *F*, plastid. *G*, ergastic material. *H*, chondriosomes. *I*, vacuole. *J*, tonoplast, or vacuole membrane. *K*, cytoplasm. *L*, ectoplast.

The two most constant constituents of the cell (Fig. 10) are the *cytoplasm*, in which other cell organs and inclusions are imbedded, and the *nucleus*, which at least in many respects is the most important of these organs.[1]

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[1] According to the older usage only the extra-nuclear portion of the protoplast was called "protoplasm," which was unfortunate because of the fact that the nucleus also is composed of protoplasm, or living substance in its broader sense. It is now the general custom to avoid this ambiguity by employing Strasburger's terms *cytoplasm* and *nucleoplasm* (*karyoplasm*, Flemming). The older usage, however, has not been entirely superseded.

The *cytoplasm*, a more or less transparent, viscous, colorless fluid, may, with its formed components and inclusions, occupy the whole volume of the cell. This is generally true of animal cells and the younger cells of plants. If much vacuolar material is present, the cytoplasm may constitute only a thin layer lining the wall, the central *vacuole* with its cell sap often far exceeding it in volume (Fig. 11, *A-C*). In many cases the cytoplasm forms a system of anastomosing strands that often show active streaming (Fig. 11, *D*). Externally the cytoplasm is limited by a specialized layer of different consistency, known generally as the *ectoplast*. Where it comes in contact with an enclosed vacuole it is also limited by a membrane, the *vacuole membrane*, or *tonoplast*. The cytoplasmic portion of the cell is often called the *cytosome*.

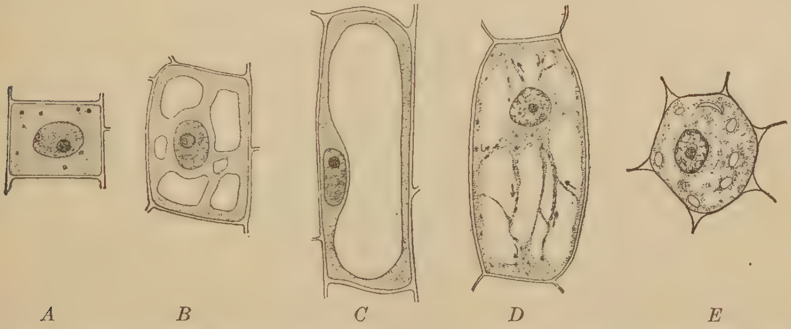

FIG. 11.—*A–C*, diagrams of a plant cell in three stages of development; the vacuoles increase in volume and the protoplasm becomes limited to the parietal region. *D*, cell of stamen hair of *Tradescantia*, showing streaming movements in cytoplasmic strands. *E*, parenchyma cell from cortex of *Polygonella*.

The nucleus comprises a ground mass of hyaline fluid in the sol or gel state, known as *karyolymph* (*nuclear sap*); an imbedded *nuclear reticulum* composed of *karyotin*, which in some way involves chromatin;[1] a limiting nuclear membrane; and usually one or more *true nucleoli*, or *plasmosomes*. Often there are present *chromocenters*, or "chromatin nucleoli," which represent accumulations of karyotin at certain points in the reticulum, and which should not be confused with the true nucleoli.

In plant cells *plastids* of one or more types are nearly always present, the most conspicuous being green chloroplasts. Plastids are very rare in the cells of animals.

A *centrosome*[2] is found in the majority of animal cells and in those of certain lower plants. It is typically made up of a central granule, or *centriole*, imbedded in a mass of hyaline or alveolar material known as the *centrosphere*, but either of these elements may be present alone. During stages of nuclear division the centrosome is surrounded by a conspicuous system of radiating *astral rays*, collectively called the *aster*.

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[1] For the use of these terms see p. 88.

[2] The terminology here differs slightly from that used in the first edition of this book (see further Chapter XI).

*Chondriosomes* have now been demonstrated in the cytoplasm of nearly all plant and animal groups. These are minute bodies having the form of granules, rods, or threads, and constitute a group of materials of uncertain function.

A common constituent of animal cells is the *Golgi material*, which occurs in the form of small bodies or more or less extensive networks in the cytoplasm. It is therefore often called the "internal reticular apparatus." It seems probable that the Golgi material is in some way related to the vacuolar material of plants.

*Ergastic substances*[1] are accumulations of nutritive materials and other products of metabolic activity. These non-protoplasmic substances, which occur chiefly in the cytoplasm and vacuoles, may exist in the form of visible granules, droplets, or crystals. Such substances may also occur in the dissolved state.

The *cell wall* of plants, as at present understood, is usually thought of not as a part of the cell proper, or protoplast, but rather as a secretion of the latter. It is often absent, as in motile spores and gametes. The *intercellular substance* of many animal tissues also bears a somewhat problematic relation to the protoplast.

It is scarcely necessary to point out that the cell should not be thought of as a static thing with a permanent physical structure. It is rather a dynamic system in a constantly changing state of molecular flux, its constitution at any given moment being dependent upon antecedent states and upon environmental conditions. In the words of Harper (1919), it is a colloidal system in which the various processes have become progressively localized in certain regions, with the resulting formation of organs, which, with the increasing constancy of the processes involved, have come to possess a permanence and individuality of their own. The characteristic organization of the cell, as has already been said, is a result of the differentiation of protoplasm, and this organization is of such a nature that it plays in turn an important part in determining the development of a higher degree of differentiation. Its efficiency in this respect is indicated by its almost universal occurrence in organisms of so many types.

**Cellular Differentiation.**—Differentiation, in the words of Conklin, is "transformation from a more general and homogeneous to a more special and heterogeneous condition." It involves the development of unlike functions and structures, and the segregation of these in different parts of the organism. Physiological division of labor and morphological division of substance constitute one inseparable process; and this process in its last analysis is the result of chemical changes in protoplasm caused by the combined action of intrinsic and extrinsic factors. Furthermore, differentiation is always associated with integration; these are two aspects of one thing, namely, organization (Conklin, 1924).

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[1] These were called metaplasmic inclusions in the first edition. See the section on Protoplasm and Metaplasm in Chapter II; also Chapter VIII.

Differentiation occurs in uninucleate cells, multinucleate plasmodia, and multicellular masses. In the bodies of certain protozoans, such as *Paramœcium* (Fig. 9), one sees within a single cell a very elaborate regional differentiation in structure, certain functions being localized in definitely constituted organs. There are distinct locomotor, digestive, and excretory systems, as well as a "neuromotor apparatus" which seems unquestionably to function as does the nervous system of larger animals.[1] These are probably the most complex cells known.[2]

The differentiation of functionally distinct regions in multinucleate plasmodia occurs not only in all cœnocytic organisms, but also to some extent in certain phases of the life cycles of multicellular forms. This matter will be considered in a later section of the chapter, where its important bearing on differentiation in multicellular plants and animals will be pointed out.

Differentiation in multicellular masses is well exemplified in the growing points of vascular plants. In the stem tip and root tip there are actively growing regions, known as *meristems*, in which the cells are in a relatively undifferentiated "meristematic" or "embryonic" condition. In many plants there is another extensive region of such cells in the cambium. As a rule, meristematic cells contain no conspicuous ergastic inclusions, and are separated by very delicate walls with no intercellular spaces. As growth proceeds the cells multiply very rapidly (hence the use of root tips for the study of nuclear division), and in certain regions somewhat removed from the region of greatest meristematic activity

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[1] R. G. Sharp (1914), Yocum (1918), C. V. Taylor (1920), Rees (1921), McDonald (1922), Kofoid and Swezy (1922, 1923).

[2] Certain writers, notably Dobell (1911*a*), hold that the protozoan body is "non-cellular" rather than "unicellular," and restrict the term "cell" to the integral parts into which a "multicellular" organism is subdivided. Whatever may be thought of the practicability of this use of terms, its theoretical implications are worthy of attention. Although agreeing with Dobell that the protozoan body and the ordinary tissue cell are not homologous, we have chosen to use "cell" more loosely as a term of convenience for both of them, as well as for other units for which morphological equivalence is not claimed. We share Doncaster's (1921) opinion that the conception of the cell, useful as it is, "no longer requires or is capable of the strict definition that was needed when the word was supposed to represent a fundamental biological entity."

It is also frequently urged that "organelle" rather than "organ" should be used for intracellular differentiations such as nuclei, plastids, and the neuromotor apparatus, and that the latter term should be applied only to multicellular structures. We have used "organ" in the more general sense in order to emphasize the fact that in all cases the structures indicated are regional differentiations of protoplasm associated with certain functions, to which the presence or absence of cell partitions is a subordinate feature. "Organelle," however, is a useful term.

(which in pteridophytes usually centers in a distinct "apical cell;" see Fig. 12) the cells gradually become visibly diversified in structure in connection with their increasing specialization in function. Throughout the active life of the plant the homogeneous meristematic cell mass thus continues to grow distally and differentiate proximally into tissues with very diverse histological characters (see Eames and MacDaniels, 1925).

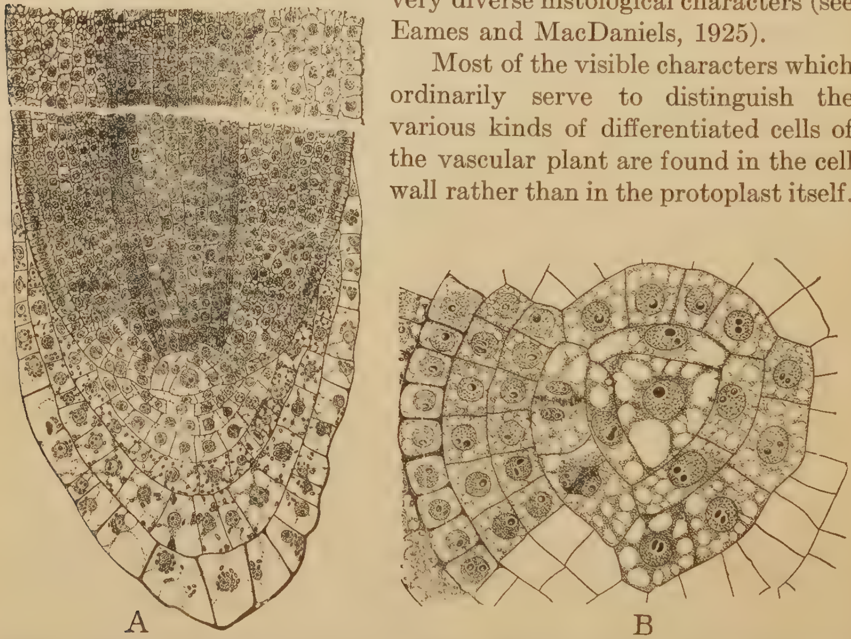

Fig. 12.—Longitudinal and transverse sections of apical meristem in root of *Pteris*, showing triangular pyramidal apical cell. The segments cut from the distal face of the cell go to form the root cap, while those from the 3 lateral faces develop into the tissues of the root proper. (*After Hof*, 1898.)

Most of the visible characters which ordinarily serve to distinguish the various kinds of differentiated cells of the vascular plant are found in the cell wall rather than in the protoplast itself. Thus besides meristematic and slightly modified parenchymatous cells there are many other types, such as tracheids, vessels, wood fibers, phloem fibers, and sieve tubes (Fig. 13), all of which are characterized by the peculiar ways in which their walls become modified through secondary and tertiary thickenings, and by the form and arrangement assumed by the pits (see p. 216). The protoplasts may finally disappear completely from wood cells, leaving a tissue or framework composed of lifeless cell walls. All functional differences are accompanied by chemical or physical differences of some sort in the protoplasm, but it is mainly in the non-protoplasmic elements (including the wall) rather than in any conspicuous structural changes in the protoplasm itself that cell differentiation is rendered visible in the case of plants. Apart from differences in shape, amount of vacuolar material, accumulated food, and other products of differentiation, protoplasts performing widely different functions may appear much alike.

Structural differentiation in connection with division of labor is very striking in the protoplasm of animal cells, which are destitute of such walls as plant cells possess. The muscle cell shows many fine longitudinal fibrils which are in some way concerned with the cell's power of contractility. In certain muscles these fibrils are so segmented that the whole

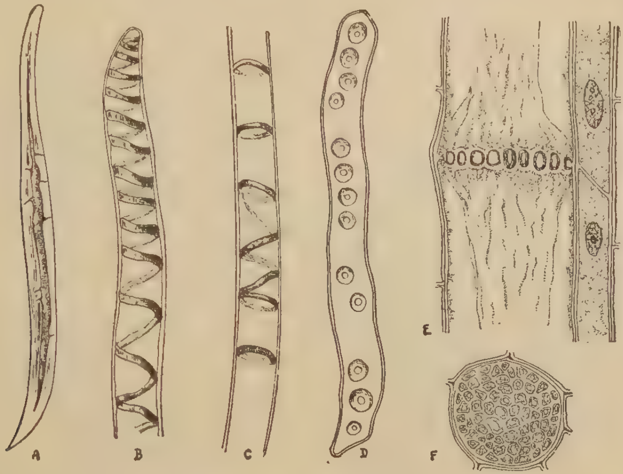

Fig. 13.—Differentiated cells from vascular plants.

*A*, wood fiber with thickened wall. *B*, *C*, portions of tracheids with spiral and annular thickenings. *D*, pitted tracheid. *E*, portion of sieve tube with adjacent companion cells. *F*, face view of sieve plate shown in section in *E*.

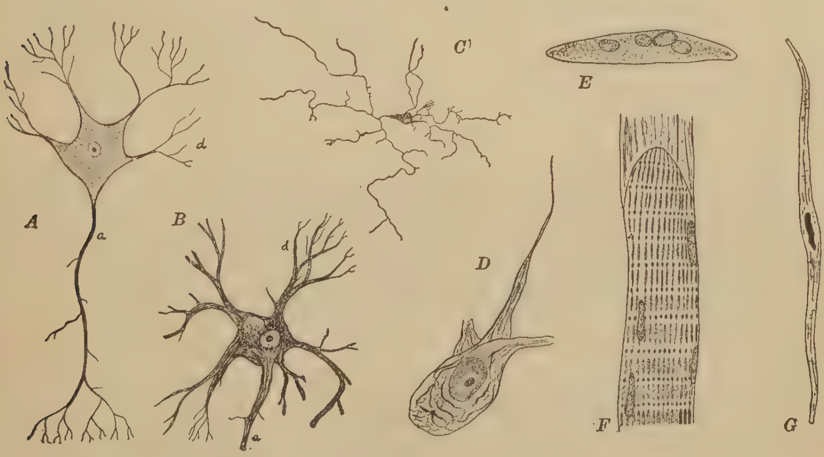

Fig. 14.—Nerve and muscle cells of animals.

*A*, diagram of a typical neuron: *a*, axis cylinder process or axon, ending in arborescent system; *d*, dendrites. (*After Obersteiner and Hill.*) *B*, cell from human spinal cord, × 75. (*After Obersteiner and Hill.*) *C*, nerve cell from the eye. (*After Lenhossék.*) *D*, Nerve cell from the earthworm. (*After Kowalski.*) *E*, young voluntary muscle cell. *F*, portion of mature voluntary muscle cell, showing striations. *G*, Involuntary muscle cell from intestine. (*E–G after Piersol.*)

cell has a transversely striped appearance (Fig. 14, $F$).[1] These transverse striations appear in living cells in tissue cultures, but there seems to be some doubt about the longitudinal fibrils (Lewis and Lewis, 1924).

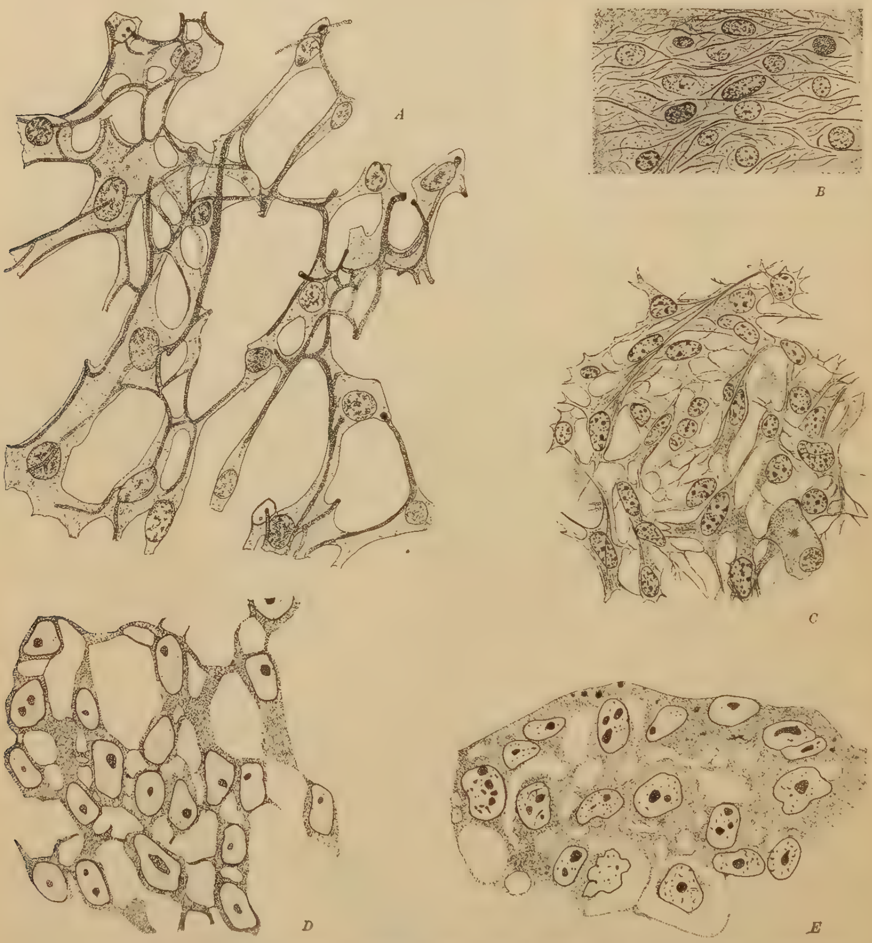

Fig. 15.—*A*, reticular connective tissue from lymph gland of cat. (*After Heidenhain.*) *B*, young heart muscle of dog embryo, showing myofibrils developing, but no subdivision into cells. *C*, later stage of same. (*B and C after Godlewski.*) *D*, development of cells in plasmodium by vacuole formation in human embryonic epithelium. (*After Marchand.*) *E*, development of cartilage tissue from plasmodium in *Lophius*. (*After Studnicka.*)

The nerve cell (Fig. 14, *A-D*) typically possesses a single unbranched prolongation (*axon*) and one or more others (*dendrites*) which often become very elaborately branched, especially in the ganglion cells of the spinal cord and brain. In fixed preparations the cytoplasm of the nerve cell contains fine “neurofibrils[1] and also granules of chromatic “Nissl substance.” It has been reported that in healthy living cells, however, the neurofibrils cannot be detected, and probably represent coagulation artifacts (Matsumoto, 1920; Lewis and Lewis, 1924; de Moulin, 1923). The naturalness of the Nissl substance is also very doubtful.

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[1] For extended accounts of these structures, see Heidenhain (1911) and Meyer (1921).

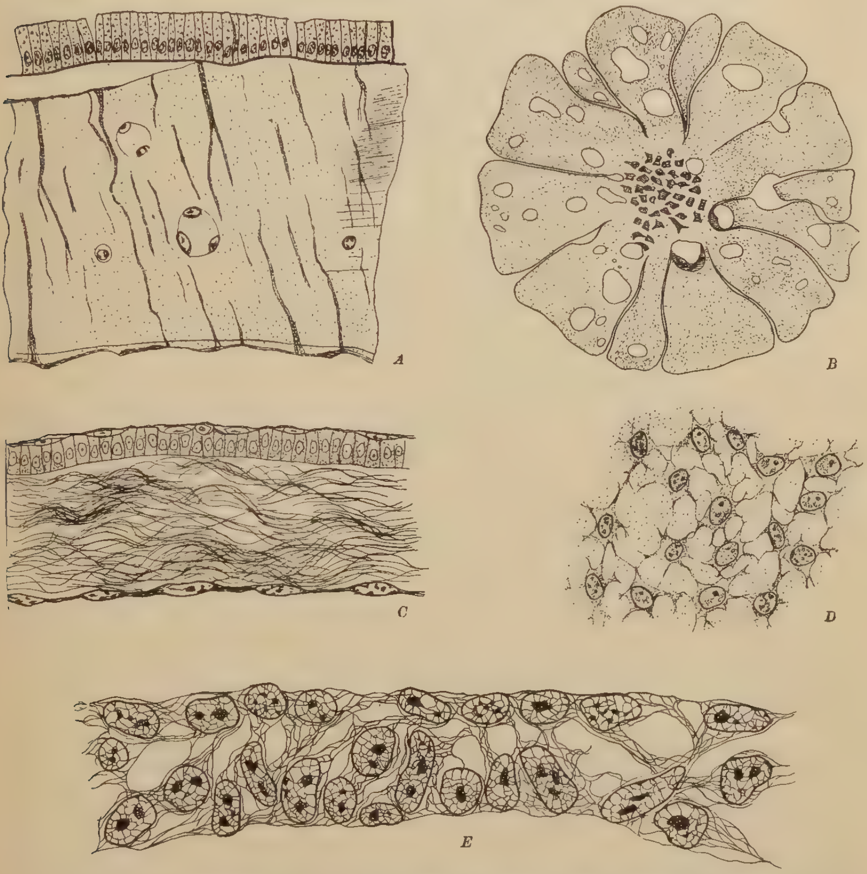

Fig. 16.—*A*, subepidermal layer of non-cellular gelatinous connective tissue in *Amphioxus*. (*After Studnicka.*) *B*, cleavage of multinuclear proembryo into cells in *Geophilus ferrugineus;* nuclei at center. (*After Sograff.*) *C*, cornea of chick embryo, showing subepidermal connective tissue with fibrils but no cellular subdivision. (*After Gurwitsch.*) *D*, connective tissue with gelatinous ground substance in lizard embryo. (*After Maurer.*) *E*, plasmodial epithelium from 2-day chick embryo. (*After Minot.*)

Cells specialized in connection with motility, such as spermatozoa (Fig. 150) and the cells of certain epithelial tissues (Fig. 151), show complex structural modifications not only in the flagella, cilia, and cirri which they bear (p. 41), but also in the other cell organs with which the activities of these motile structures are closely connected (see Chapter XIV).

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[1] See Heidenhain (1911).

Secretory cells are often distinguishable not only by the accumulations of secretion products in their cytoplasm, but also by the peculiar form assumed by their nuclei (Fig. 24, *A*, *C*).

In connective tissues (Figs. 15, *A* and 16, *D*) the protoplasm is subdivided into cells with various degrees of distinctness, depending on the amount of metaplasmic supporting substances produced during their differentiation. Cartilage and bone cells are likewise imbedded in such metaplasmic substances (Rohde), which are here produced in relatively enormous amounts and later form the main supporting framework of the body. Blood, which is sometimes spoken of as a "fluid tissue," consists of a plasma with floating cells of a variety of types.[1]

Differentiation in a multicellular mass, involves the gradual setting apart of special regions with modified structural and functional characters, as in the body of a protozoan, but with the important difference that these regions include many cells, each of which retains in some degree the fundamental type of protoplasmic organization (nucleus, cytoplasm, semi-permeable membranes) possessed by the cell which began the development of the differentiating mass. One therefore expects a greater capacity for independent action in these cellular components of the body than in the subcellular components of the protozoan body. This expectation is fulfilled in the results of experiments which have shown that many tissues and cells of higher organisms may, if given structural independence and a proper environment, continue to live or even in many cases to grow into a complete new body. The ability of such an isolated part to reconstitute a whole depends upon the measure in which it has retained what is fundamental in the physico-chemical constitution of protoplasts through the period of its differentiation. This leads to a consideration of certain physiological characteristics of differentiating cells.

**Differentiation and Senescence.**—The structural and functional modification of tissues and the accumulation of the products of metabolism are aspects of the phenomenon of senescence. As life progresses, the body tissues gradually "age," and if nothing prevents it the process eventually terminates in protoplasmic disorganization and death. What shall be taken as an index of the degree of senescence has been the subject of much discussion.

Child (1915) has brought forward much evidence to show that the relative rate of metabolism is the main criterion of physiological age, "young" cells having a high rate and "old" cells a relatively low rate, and a gradual decline in this rate occurring throughout the life of the cell. In embryonic (physiologically young) cells the cytoplasm appears to be comparatively homogeneous and undifferentiated. Older cells, on the contrary, are ordinarily marked by the presence of products of differentiation in the cytoplasm. The true measure of age is, therefore, not time, but physiological differentiation.

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[1] For the literature pertaining to the morphology of the blood, see Lambin (1923).

In many cells a rejuvenating process may occur, whereby a high metabolic rate is restored and the products of differentiation reduced in amount. This is regarded as "a return to the embryonic state"—a real physiological rejuvenescence. Such a rejuvenescence occurs in connection with regeneration, vegetative and other asexual reproduction, and sexual reproduction. In each case the tissue or cell which begins the new life cycle—the meristematic regenerating cells, the zoöspore, or the zygote—has a relatively high metabolic rate. Conklin (1912, 1913) has emphasized the importance of the rate of interchange between nucleus and cytoplasm in connection with senescence and rejuvenescence.

In many lower organisms differentiation in this sense is not so great but that almost any cell may retain the power to "dedifferentiate" and begin the development of a new individual vegetatively. In these forms asexual reproduction may occur repeatedly and keep the organism as a whole (in Protozoa and Protophyta) or the protoplasm of the race (in lower Metazoa and Metaphyta) physiologically young. Only when the metabolic rate falls very low does sexual reproduction, the most effective of all the rejuvenating agencies, or, in certain Protozoa, a special process known as endomixis, ensue.

In the higher plants the retention of the power of dedifferentiation is strikingly shown in the well-known cases of *Begonia* and *Bryophyllum*, which can regenerate complete new individuals from a small bit of leaf tissue. In the higher animals differentiation is usually so great that the somatic tissues can no longer dedifferentiate and reproduce the organism asexually. Here rejuvenation occurs only after the union of two gametes, which are themselves, unlike the zoöspores of algæ, physiologically old. Although local rejuvenescence may occur, as in secretory cells which are "younger" after secretion, and also in wound tissue, the differentiation of the body cells is carried so far that their metabolic rate falls low enough to make a recovery or rejuvenescence no longer possible. Thus it is only the functioning reproductive cells that endure; the ultimate cessation of all life processes in the body is the price which is inevitably paid by the complex multicellular organism for the advantages conferred by its high degree of differentiation.

Of the highest importance in this connection are the results of attempts to maintain the cells and tissues of higher animals in the living condition in artificial culture media outside the body. It has been shown by the remarkable experiments[1] of R. G. Harrison, Carrel, Leo Loeb, Burrows, H. V. Wilson, W. H. and M. R. Lewis, and others, that small pieces of the essential differentiated tissues of the body may be isolated and kept actively growing *in vitro* for a length of time frequently far exceeding the normal life period of such tissues in the body. The cells in such cultures show certain capacities for behavior not ordinarily realized in their more normal environment, and in one or two instances have been seen to undergo a certain amount of differentiation and dedifferentiation; but in general they tend strongly to maintain their characteristic types of structural differentiation. They do not appear to grow old; indeed, it is not improbable that in a constantly favorable environment somatic cells are as "potentially immortal" as germ cells have been claimed to be (see Chapter XXI). It thus appears that the senescence and the death of the metazoan body are results of the extreme differentiation and specialization of mutually dependent tissues and cells, and that the fundamental vital process is not of itself inevitably mortal in character (Pearl, 1921).

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[1] For a general account, see Lewis and Lewis (1924).

**Protoplasmic Continuity.**—Any consideration of the means by which correlation is maintained between the parts of the highly differentiated plant or animal body must obviously be founded upon the structural interrelations of these parts. All of the cells of the body are in very intimate physiological connection, and it is not improbable that this in most cases involves an actual protoplasmic continuity.

*Plants.*—The presence of delicate connecting strands in plant tissues was suspected long before they were seen, and even the coarse strands in sieve tubes, though often observed, were not well known until the time of Sachs and Hanstein (1864). The existence of fine protoplasmic connections in many plant tissues was demonstrated in a large number of researches between 1880 and 1900.[1] Poirault and Gardiner showed that they occur throughout the body in pteridophytes and gymnosperms, and it is probable that the same is generally true of the angiosperms.

In plants two general types of connecting strands are found. In the red algæ and certain other thallophytes adjacent cells communicate through one relatively large pore which is left as the result of incomplete wall-formation. Materials may later be deposited in such pores, reducing the connections to fine strands. Large strands are also found in sieve plates, laticiferous vessels, and between the egg and surrounding cells in cycads; but these seem to be due either to the enlargement of smaller pores present at an earlier stage, or to actual solution of the intervening wall. Strands of the second general type, which are known as *plasmo-*

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[1] Among these may be mentioned the works of Wille (1883) and Borzì (1886) on the Cyanophyceæ; Kohl (1891), Overton (1889), and Meyer (1896) on the Chlorophyceæ; Hick (1885) on the Fucaceæ; Hick (1883), Massee (1884), and Rosenvinge (1888) on Florideæ; Kohl (1897) on mosses; and, on vascular plants, those of Tangl (1879), Russow (1882), Strasburger (1882, 1901), Goroschankin (1883), Terletzki (1884), Wortmann (1887, 1889), Haberlandt (1890), Kienitz-Gerloff (1891), Jönsson (1892), Kuhla (1900), Poirault (1893), Gardiner (1884, 1897, 1900), Hill (1900, 1901), Gardiner and Hill (1901), and Kohl (1900, 1902). For general accounts of protoplasmic connections, see Davis (1905), Meyer (1920), and Lundegårdh (1922).

*desma*, are of exceedingly small diameter, special methods being required for their demonstration (Fig. 17). They may be distributed rather uniformly over the wall, or they may be aggregated in small groups, which are often located in pits or thin spots; frequently they are branched. They consist of a hyaline substance which may possibly be simply ectoplasm, and at the middle point there is often a small swelling.

Very little is accurately known regarding the origin and development of plasmodesma. It can scarcely be doubted that the pores through which they pass are often present from the time the cell partitions are first formed, no wall substance being deposited at these points. It has been the opinion of some investigators (Tangl, Russow, Gardiner) that they arise directly from the median portion of the spindle fibers at the close of mitosis, but others (Kienitz-Gerloff, Strasburger, Meyer) have opposed this particular interpretation. There is also considerable evidence in support of the view that plasmodesma are secondarily developed structures. Strasburger (1901) stated that extensions from adjacent cells come into contact as the intervening wall begins to thicken, but do not form continuous strands. The fact that in separating cells the break occurs through the thickened median portion of the strands lends support to this view (Hume, 1913). That the strands are actually continuous was emphasized by Meyer (1896, 1902, etc.), who held that they are due both to retention and to new formation. He observed their secondary formation in *Volvox* and in fungus hyphæ which came in contact.

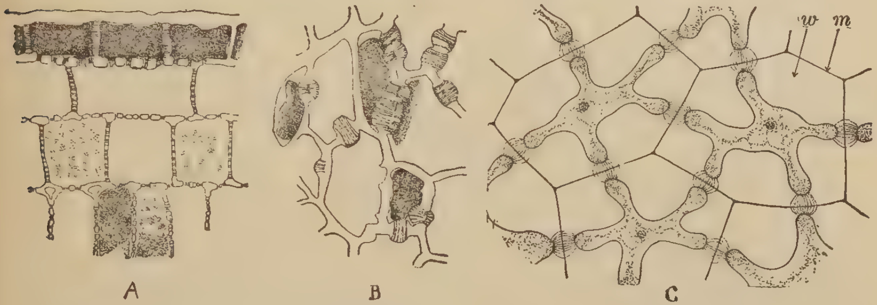

Fig. 17.—Plasmodesma in vascular plants. *A*, *B*, cells in cotyledon of *Pinus*. (*After Gardiner and Hill*, 1901). *C*, endosperm cells of *Phytelephas* ("vegetable ivory"): the walls (*w*) are greatly thickened, and the protoplasmic continuity is maintained through bundles of delicate strands. *m*, middle lamella.

Light on this question has been sought in parasites and graft hybrids, where cells of different species come together. Kienitz-Gerloff, Kuhla, and Strasburger found no plasmodesma between the cells of *Viscum* and *Cuscuta* and their hosts, but in the case of graft hybrids both Buder (1911) and Hume (1913) report their presence in the walls separating cells which are supposed to be genetically unrelated. This seems to show that connections may arise secondarily, although uncertainty regarding the exact behavior of the protoplasts in the wounded region leaves an element of doubt.

At present the probabilities are in favor of the view that intercellular connections are both primary and secondary in origin, some of them representing regions in which the continuity of the protoplasm has never been broken, and others being subsequently developed through the intervening cell membranes. The very fact that a given area of cell wall becomes enormously extended during the growth of the tissues indicates that many of the pores seen at maturity must have been formed anew. It is also to be remembered that at the time when pore formation would necessarily occur the cell membranes are very thin and gelatinous, and would offer little resistance to dissolution or penetration by the protoplasts. Thus the fact that cells may glide or roll over one another during the early stages of development does not prove the impossibility of protoplasmic continuity between them. The exceeding fineness of many known plasmodesma, moreover, indicates that failure to find such connections in certain tissues does not necessarily prove their absence.

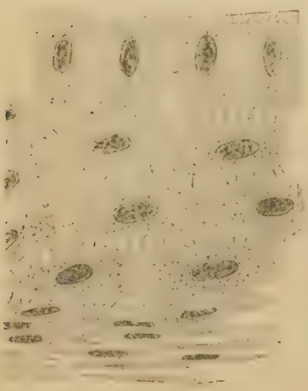

FIG. 18.—Protoplasmic continuity in human mesoderm tissue. (*After Maurer.*)

*Animals.*—Protoplasmic connections have been rather widely described in animals, and are best known in epithelial, muscle, and connective tissues (Fig. 18). In connective tissue they may be broad cytoplasmic extensions, giving the tissue the character of a protoplasmic net-work (Fig. 15, *A*), or they may be very fine threads. As in plants, they are the result of either an incomplete division or a fusion of cell outgrowths. The fact that cells in animals are mostly divided by a process of furrowing indicates that connections, if present, must be for the most part secondarily developed. In his study of living tissues, Chambers (1924) finds in the majority of cases no direct evidence of protoplasmic bridges, and is inclined to agree with certain other workers in interpreting many reported connections as either fixation artifacts or fibrous differentiations in the intercellular substance, rather than actual protoplasmic strands. Such strands are clearly present, however, in squamous epithelium (Chambers and Rényi, 1925). Some investigators, as will be pointed out in a subsequent section, regard the intercellular substance itself as living matter of a special kind. The establishment of protoplasmic connections between blastomeres has been described (G. F. Andrews, 1897; E. A. Andrews, 1898, Shearer, 1906). Chambers, however, fails to find them.

*Function.*—It can scarcely be questioned that plasmodesma serve to transmit stimuli of one kind or another from cell to cell (Pfeffer, 1896). Noteworthy in this connection is their presence in tissues of plant parts known to be particularly responsive to external stimuli, such as the leaves of *Mimosa* (Gardiner, 1884) and *Dionæa* (Gardiner, 1884; Macfarlane, 1892), the stamens of *Berberis* (Gardiner, 1884), and the sensitive labellum of the orchid, *Masdevallia muscosa* (Oliver, 1888). The effects of mechanical injury appear to be transmitted through epithelial tissue by way of such intercellular bridges, according to Chambers and Rényi (1925). Their extensive development in storage tissues, such as the endosperm of seeds (Tangl, 1879; Gardiner, 1897), would also suggest that they are in part responsible for the readiness with which nutritive materials are translocated in such specialized tissues.

The chief significance of protoplasmic connections of all types lies in their coördinating function. No such degree of differentiation and specialization of tissues as we see in higher organisms could be attained, and no such complex mechanism could continue to act as a unit or individual, were it not for adequate means of keeping the various parts fully correlated in action. The importance of connecting strands should, therefore, be evident. The protoplasm of the entire individual is more or less continuous from the beginning of the ontogeny onward. It should not be thought, however, that without such connections there can be no correlation. Mere contact is sufficient for the passage of electrical stimuli, which, as will be indicated below, are becoming increasingly recognized as of importance in the development and operation of the body. Cells separated by delicate colloidal membranes with no actual protoplasmic continuity are still able to interact and influence each other's behavior to a considerable degree. Thus without protoplasmic continuity the cells may have a physiological continuity; and it is the possession of both that conditions the coördinated action of most tissues. In any case the field of force which pervades the whole organism and which shapes its development is not interrupted by cell partitions (Thompson, 1917).

**Correlation and Polarity.**—Reference has been made in the preceding paragraph to the dependence of differentiation on correlation, or integration, no multicellular individual being possible unless the diverse activities of its many parts are kept mutually adjusted. The significance of protoplasmic continuity and the nervous system as coördinating mechanisms has been pointed out. Another means of correlation is seen in hormones. These are chemical substances produced in certain parts of the body and sent into the blood stream, which carries them to other parts upon whose activities they have profound effects. The question of the action of similar substances in the plant body is an open one; Loeb (1915, 1921*b*) has emphasized their probable rôle.

One of the most suggestive conceptions in this connection is that developed by Child (1911, etc.) and his associates. It has been shown in a number of animals and plants that along each of the axes of symmetry there exists a *physiological gradient* (also called "metabolic gradient" and "axial gradient"): the rate of the physiological processes is highest at one end of the axis and diminishes progressively toward the other end. The anterior end of a planarian, for example, exceeds the posterior end in its rate of oxygen consumption and carbon dioxide output, and in its susceptibility to poisons. Furthermore, the portions of higher rate have a "dominating" influence over the development of those portions having a lower rate, with the result that the young individual soon develops and maintains a definite physiological correlation of anterior and posterior parts. Similarly, in individuals with more than one axis of symmetry, there may be a corresponding dorsal-ventral, as well as an axial-marginal, correlation. Cases are known in which there are two regions of high rate along one axis (Hyman, 1916, 1921; Hyman and Bellamy, 1922). The gradient arises in the first place, according to Child, as a response to differential factors in the environment; and although the types of organs developed depend upon the hereditary constitution of the organism, their arrangement and mutual behavior are due in large measure to the gradient. This is indicated by the fact that experimental alterations in the metabolic rate along the axis are followed by the expected abnormalities in structural development.

As to the means by which different regions along an axis influence one another, Child adduces evidence in support of the theory that the fundamental relations of polarity "depend primarily upon impulses or changes of some sort transmitted from the dominant region, rather than upon the transportation of chemical substances" (1915, p. 224). Very significant in this connection is the fact that there is a definite relation between physiological gradients and electrical polarity. The dominant and less active regions are respectively the negative and positive poles of the living system. Where the current enters the protoplasm from the exterior (negative pole) anabolic processes are promoted through increased oxidation, and where it leaves (positive pole) catabolic processes are furthered.[1] Alterations in electrical polarity are accompanied by alterations in the mode of growth.[2] Thus, in the opinion of Lillie (1923), "bioelectric currents exert a controlling and coördinating influence in normal growth processes as well as in normal stimulation."

It cannot at present be said to what extent this particular conception of polarity is applicable to the single cell. In the early days of cytology two groups of workers emphasized respectively the importance of morphological and physiological polarity within the cell (see Wilson, 1900, p. 55).

[1] Hering (1888), Mathews (1903), R. S. Lillie (1919, 1922, 1923).

[2] Bose (1918), Ingvar (1920), Lund (1921).

Since that time it has been shown that the structural and functional axes coincide, which indicates that the two are but different aspects of one and the same polar differentiation. The origin of polarity in the animal egg cell is of considerable importance. Some investigators think it not improbable that it is in some way carried over from the preceding generation (see Conklin, 1924), but the more prevalent view is that it arises secondarily as a response to some environmental factor (Child; Bartelmez, 1912; B. G. Smith, 1922).

It is too early to judge the relative importance of the many factors which appear to have effects on polarity and other features of differentiation. Some investigators are inclined to view physiological gradients as results rather than causes of polar differentiation, at least in certain cases (R. G. Harrison, 1921; Kingsbury, 1924), and the electrical phenomena involved are yet but little known. It is clear, however, that hypotheses involving physiological and electrical gradients are contributing much toward a solution of the problems of differentiation and correlation.

**The Cell Theory and the Organismal Theory.**—The fact that the body of a higher organism comprises a vast number of semi-independent specialized parts, the cells, led many years ago to the formulation of two general theories which differed fundamentally in their interpretation of the relation existing between the two individualities: the organism as a whole and the cell. These theories are known as the Cell Theory and the Organismal Theory.[1]

*The Cell Theory.*—The foundation of the Cell Theory in 1838 and 1839 by Schleiden and Schwann, and its dominant influence upon biology throughout the nineteenth century have been briefly discussed in Chapter I. The principal propositions involved in the theory are summarized by Heidenhain (1907, p. 29) essentially as follows: All living substance is concentrated in cells; the cells of the body are all individuals of the same morphological rank; the tissue cell is morphologically and physiologically an elementary individual, the unit of structure and function; the body is an aggregate of cells, which are its "building stones;" the action of the body is the sum of the many special actions performed by collaborating cells of many kinds. According to this theory, therefore, the cell is the fundamentally important individual—the "primary agent of organization." In the ontogeny the multiplying elementary organisms, the cells, coöperate to build up an individual of a higher order, the multicellular organism. Such an organism is thus a "cell state," or "cell republic," secondarily formed by the aggregation of a vast number of elementary individuals.

The phylogenetic aspect of the Cell Theory developed when it was discovered that many minute organisms are single uninucleated masses of protoplasm much like the constituent cells of the multicellular forms.

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[1] See footnote on p. 17.

It was concluded that such "unicellular elementary organisms" have in the course of time formed loose colonies, either by direct aggregation or by an acquired failure to separate after a period of multiplication: and that the individual units have become increasingly interdependent and knit together until individuals of a higher grade, multicellular organisms, have resulted. "Each cell," said Schleiden, "leads a double life: an independent one, pertaining to its own development alone; and another incidental, in so far as it has become an integral part of a plant." As a consequence of this interpretation the individual protozoan has been homologized with a single cell of the human body. The dominance of the Cell Theory, moreover, has resulted in the tendency to describe everything of a biological nature so far as possible in terms of cells.

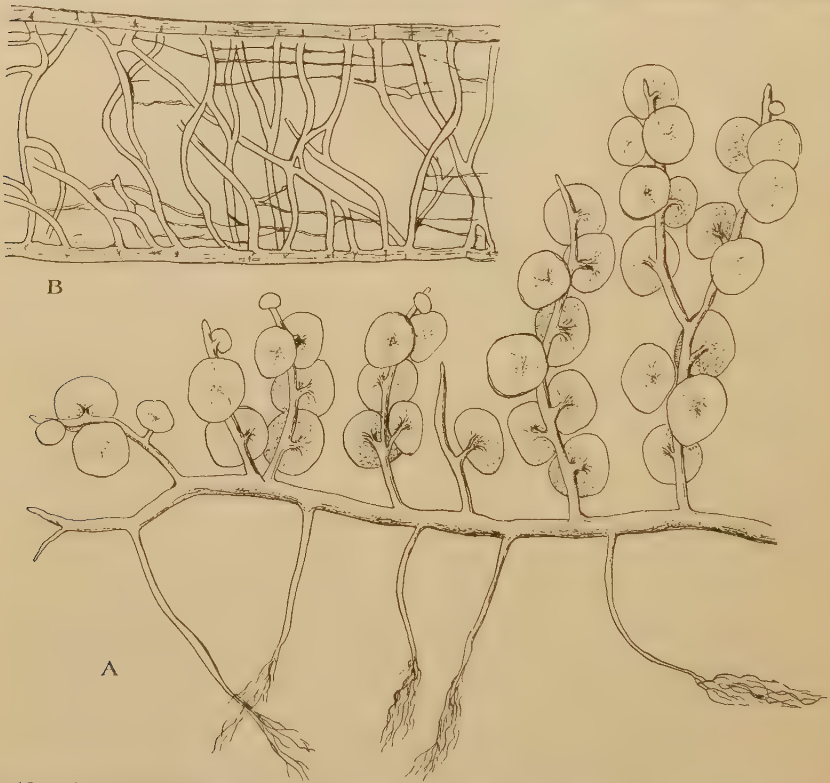

Fig. 19.—*A*, *Caulerpa macrodisca*, a cœnocytic plant. *B*, section of leaf of *Caulerpa prolifera*, showing supporting trabeculæ. (*After Oltmanns.*)

It has always been very difficult to make any plausible interpretation of plasmodial or cœnocytic organisms in terms of the Cell Theory. Such organisms are multinucleate and non-septate masses of protoplasm, which nevertheless build up bodies of definite form and with a considerable degree of differentiation (Fig. 19). If the entire cœnocytic body be regarded as one huge cell, as some have said it should be, then any limited mass of protoplasm is a cell, and cells are not everywhere morphologically equivalent as the founders of the Cell Theory maintained. The bodies of *Vaucheria*, *Cladophora*, and *Stigeoclonium* are surely homologous, which also rules out the morphological equivalence of all "cells." Others have taken the standpoint that in such cœnocytic bodies each nucleus with the portion of the cytoplasm it influences represents a cell unit; this is the energid concept of Sachs (1892, 1895). Whatever may be the actual origin of the cœnocytic condition in any particular case—whether by a fusion of cells followed by growth (myxomycete) or by the growth of an originally uninucleate mass (cœnocytic alga)— it is clear that no cell boundaries are present; in the myxomycete they have been entirely obliterated, and in the alga they have never been present. The nuclei are centers of action whose different reactions influence the cytoplasm to different distances, especially in those forms in which their position is being constantly changed by protoplasmic streaming. Such bodies have indefinitely limited centers of activity, but these are not cells.

The one constant thing in organisms of all types of differentiation is protoplasm. Since the cellular condition may be absent or developed in such different degrees by organisms otherwise so much alike (compare *Vaucheria*, *Cladophora*, and *Stigeoclonium*), it seems only reasonable to assign primary rank as an individual to the protoplasmic mass as a whole, to which cells, when present, are subordinate, though of acknowledged importance. This is the standpoint of the Organismal Theory.

*The Organismal Theory.*—The early dissatisfaction with the conception of the cell as the primary and universal agent of organization led to the formulation of the Organismal Theory, in which the emphasis was placed on the living mass as a whole, rather than on the constituent cells.[1] According to this general interpretation, ontogenesis is a function primarily of the organism as a·whole, and consists in the growth and progressive internal differentiation of a single protoplasmic individual, this differentiation often, but not always, involving the septation of the living mass into subordinate semi-independent parts, the cells. Since the septation is rarely complete, all parts remain in connection and the whole continues to act as a unit. Thus development is not primarily the establishment of an association of multiplying elementary units to form a new whole, but rather the resolution of one whole into newly formed parts: it should be thought of not as a multiplication and coöperation of cells, but rather as *a differentiation of protoplasm.* A little consideration will show that this is not a mere matter of words. "The real unity is that of the entire organism and as long as its cells remain in continuity they are to be regarded not as morphological individuals, but as specialized centers of action into which the living body resolves itself and by means of which the physiological division of labor is effected" (Wilson, 1893).

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[1] For a list of biologists who developed and supported this theory, see p. 17. The best recent exposition of the theory is that of Rohde (1923). See also Whitman (1893), Sedgwick (1894), Dobell (1911), and Ritter (1919).

Some of the evidence upon which this conception is based may now be passed in brief review.[1]

In the first place, an immense amount of development and differentiation occurs in organisms without any cell-formation whatsoever. Attention has already been directed to the Protozoa, whose bodies may show a high degree of differentiation into organs performing special functions, all within the limits of a single cell. In the eggs of many animals visible regions developing into certain parts of the organism are set apart before the egg divides, or even before fertilization. The egg is the organism in the one-cell stage, and the differentiation of its embryonic parts may be seen beginning before its subdivision into other cells begins. Most striking are those organisms that are cœnocytic throughout development. In the Siphonales, for example (Fig. 19), the body may become well differentiated into "roots," "stems," and "leaves," yet there is no cell-formation within the plasmodial body except when reproductive cells are produced. In a number of cœnocytic plants, moreover, the spores and gametes themselves are cœnocytic ("cœnogametes" in *Mucor* and *Albugo bliti;* zoöspores in *Vaucheria*). The plasmodium of a myxomycete, although it may be initiated by the fusion of a number of cells (myxamœbæ), undergoes the rest of its growth and develops its highly characteristic fruit bodies in the non-cellular condition; the only definite cells are the spores, which are delimited after the fruit body is practically completed.

Many organisms which are cellular throughout the greater portion of the life cycle pass through a cœnocytic phase, often at a critical stage in the cycle, and in this phase as elsewhere growth and differentiation continue. In vascular plants may be cited the female gametophytes of gymnosperms and angiosperms, and the embryos of gymnosperms. In the young embryos of *Dioön*, *Pinus*, *Stangeria* (Fig. 20), and *Agathis* (Fig. 21) the characteristic mode of development is indicated by the positions taken up by the nuclei during the cœnocytic stage, the position of the subsequently formed cell partitions being determined by differentiations occurring in this stage. Similarly, there are among animals cases in which the embryo first passes through a free-nucleate stage, subdivision into cells occurring after differentiation, particularly that of the germ region, is well on its way (Fig. 210). That differentiation in such cases is a function of the protoplasmic mass as a whole is indicated by the fact that any nuclei which happen to enter the germinal region become germinal nuclei, the rest becoming somatic nuclei (Huettner, 1923, on *Drosophila;* see Chapter XXI). In many such eggs the cleavage is at first only superficial, the walls forming without reference to the nuclei or their division, and the resulting compartments remaining for a time open into the common underlying mass of protoplasm (Fig. 210). Of special interest is the case of *Chætopterus,* in which eggs have been observed to differentiate into swimming larvæ even when the usual cytoplasmic

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[1] This will involve a number of matters with which the student at this point may be unfamiliar. This section should, therefore, be reread after the rest of the book has been covered. The same may also be said of Chapter I.

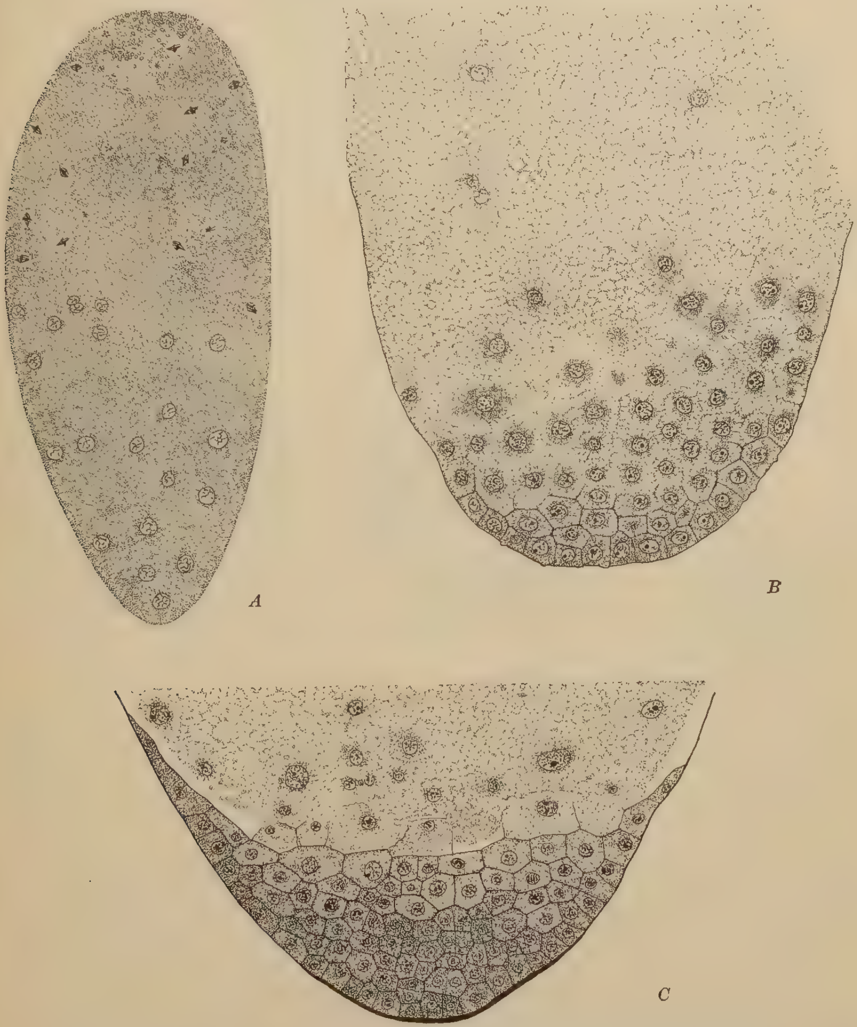

FIG. 20.—Early stages in the embryogeny of *Stangeria.* *A,* cœnocytic stage. *B,* subdivision of basal portion into cells. *C,* embryonic tissue established and showing some differentiation. (*After Chamberlain,* 1916).

cleavages are suppressed by adding potassium chloride to the sea water (F. R. Lillie, 1902, 1906).

Not only the embryo as a whole, but also many of the special tissues of the animal body may begin their development as plasmodial masses in which cellular differentiation occurs later (Figs. 15, 16). In some tissues the non-cellular condition may remain until maturity, as in certain "syncytial" types of connective tissue (Fig. 15, *A*). Rohde (1923) strongly insists that tissue formation always begins thus in a multinucleate protoplasmic mass, and that when cells are formed they always remain connected in some degree (except in free cells, such as blood cells and reproductive cells). Furthermore, the internal structures characterizing many tissue cells, such as neurofibrils, contractile fibrils, elastic fibrils, and the like, are metaplasmic differentiations (see p. 48) arising in the protoplasm before the subdivision into cells; they are formed by a plasmodium, and not by the cells. Rohde points out that in such a tissue as cartilage the metaplasmic material between the cells is not formed by the cells themselves, but by the antecedent plasmodium, the cells being the remaining masses of unmodified protoplasm (Fig. 15, *E*). "So it is not the cells that play the principal rôle in histological differentiation of animals, but the multinucleate plasmodium, not the cell-formation, but the functional differentiation of the living mass, *i.e.*, the multinucleate plasmodium forms the guiding principle in the development of organisms" (Rohde, 1908).

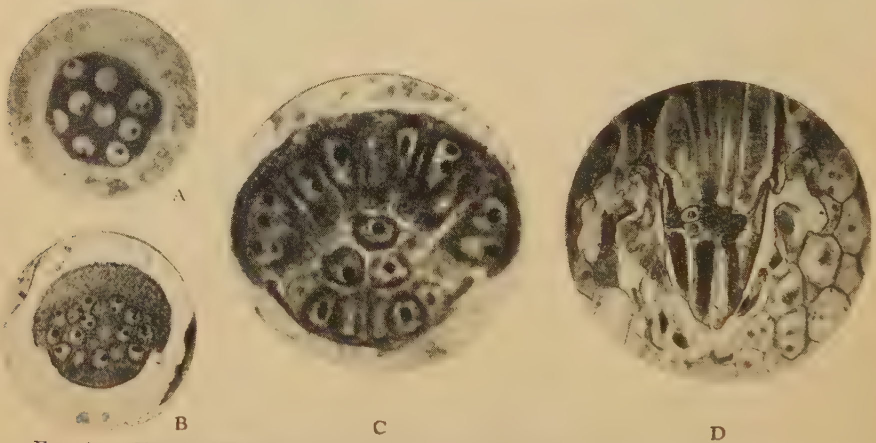

FIG. 21.—Early stages in the embryogeny of *Agathis australis*. *A*, cœnocytic stage. *B*, 32-nuclear stage with cytoplasmic suspensor cap differentiated. *C*, proembryo subdivided into cells. Three regions distinguishable: suspensor initials above, embryo proper in middle, and embryonic cap below. *D*, later stage; cap well developed and suspensor elongating. (*After Eames*, 1913.)

The fact that the same result may be achieved with or without cell-formation is of significance in this connection. The bodies of *Vaucheria*, *Cladophora*, and *Stigeoclonium* show about the same degree of elaboration, so far as essentials are concerned; yet the first is cœnocytic, the second has multinucleate subdivisions, and the third uninucleate ones. Whitman (1893) cites the case of membranellæ in *Cyclas* and *Stentor;* in the former the organ is a complete cell, whereas in the latter a whole crown of them are produced as parts of one cell, yet they otherwise show close agreement in form and structural detail in the two animals. Cells themselves differ rather widely in the mode of their formation. Their origin by division is well known, and it is sometimes said that they always arise in this way. This statement may appear in a new light when it is recalled that cells may form in multinucleate plasmodia (*a*) independently of the nucleus and its division: through the appearance of metaplasm (cartilage), through the development of membranes (heart muscle; discoidal cleavage; certain cases in thallophytes and in endosperm), or through the development of furrows or vacuoles (spores of some thallophytes; reproductive cells of certain lower animals; epithelium, mesenchyme, and connective tissue); or (*b*) independently of nuclear division, but under some nuclear influence: through formation of a special substance, usually in the form of membranes, in positions clearly determined by the location of the nuclei (most cases of embryogeny in gymnosperms and of female gametophytes in both gymnosperms and angiosperms; ganglion cells; ascospores), or through the appearance of protoplasm about the nuclei in a metaplasmic mass (peculiar case in cartilage; tooth tissue) (Rohde, 1923). Such phenomena point to the conclusion that cells are not everywhere morphologically equivalent, as Schwann held, and that they are the result of differentiation rather than its cause.

Of the highest interest are the many experiments which have been performed with cleaving animal eggs with the purpose of determining the rôle of cells in development. Although eggs of different species show different responses to experimental conditions, it has been shown in a number of cases that alterations in the position of the successive cleavage furrows do not disturb the normal course of development and differentiation. In the frog, for example, "normal development does not depend upon a specific number and succession of cleavages in definite positions but rather upon an egg pattern which may be cut up by the cleavage furrows in various ways without destroying the pattern or the normal results of development" (Conklin, 1924). The special developmental potencies of particular blastomeres (see Chapter XXI) depend upon the degree in which the cleavages setting them apart coincide with the differentiations already present and often visible in the egg. In *Styela* this correlation is very close, altered cleavages giving abnormal embryos, but in other cases it is not so. Certainly, cleavage does not determine the pattern of the embryo. Spemann (1918, etc.) has shown that in amphibian embryos groups of cells may be cut out and reversed in position or transplanted in other regions, whereupon they develop as parts of the organs normally differentiating in those regions and not as those of the regions from which they came. Thus, as F. R. Lillie (1902) concluded for *Chætopterus*, "the process of cell-division, as such, is necessary neither to growth, differentiation, nor the earliest correlations; but it is accessory, in Metazoa, to all three as a localizing factor, often from the earliest stages."

It was to the same conclusion that W. Hofmeister, Sachs, de Bary, and other botanists were led many years ago through detailed studies of cell-formation in the growing regions of plants. They found the growth of the organ as a whole to be the primary matter, the position of the cell walls within it being secondarily determined by the physical forces acting within the growing mass. "The formation of new cells in the vegetative point is accordingly a function of the general growth, not its cause" (Hofmeister, 1867). This view has been upheld by many researches on the mechanics of growth and form (see Thompson, 1917).

The phylogenetic implications of the Organismal Theory may now be pointed out. Briefly stated, the idea is that if multicellular organisms have arisen from unicellular forms, the process has been the same as that seen in ontogeny: the growth, differentiation, and subdivision of a continuous mass of nucleated protoplasm into a system of uninucleate cells. The ability of isolated tissue cells to live independently does not prove that independent cells have combined to form the multicellular body, but only that such parts can still carry on essential protoplasmic functions. The phenomenon could as well be taken to prove the derived nature of Protista. *The body is not an aggregation of elementary organisms, but a single organism which has evolved an internal cellular structure.* If the septation coincided with nuclear division from the first, there was a direct transition to forms with several cells. If the two processes did not so coincide, cœnocytic or "plasmodial" types arose, some of which persisted as our cœnocytic organisms, while others developed internal walls and became our multicellular forms. All degrees of correlation between nuclear division and cell-formation are seen in various algæ, giving bodies with constituent cells of different morphological rank, and in the embryos of vascular plants, some of which have a free-nuclear stage while others do not. The cœnocytic Siphonales have no internal walls, or only cellulose trabeculæ (Fig. 19), whereas in the lower Siphonocladiales there are transitions between this condition and the regularly walled condition seen in the higher members of the group. This suggests that mechanical support is one of the chief functions in connection with which cell walls were developed in plants. The other important function, that of delimiting functionally specialized regions, has been mentioned, and is of significance in both plants and animals.

Evolution has, therefore, occurred not by an aggregation of many units, but by the differentiation of one; not by combining cells, but by differentiating protoplasm. The cell colonies in the Volvocales and the remarkable polyp colonies in the Siphonophora (see J. S. Huxley, 1912) show the possibility of an evolution by the combination ol individuals, but it is not at all clear that they afford the key to the evolution of organisms in general. The protozoan is properly regarded as homologous with the whole man; both are organisms which have differentiated a series of specialized internal regions or organs, the one without cellular subdivision or increase in size, and the other with them.

**Conclusion.**—In the present chapter we have stressed the importance of the conception of the organism as essentially a mass of nucleated protoplasm which has undergone internal functional and structural differentiation. This differentiation in different cases has involved no multiplication of nuclei or cellular subdivision and very little increase in size ("unicellular" Protista); or multiplication of nuclei and considerable growth without cellular subdivision (cœnocytes); or both nuclear multiplication and various degrees of cellular subdivision, with much growth ("multicellular" organisms). The principle of functional protoplasmic differentiation is more general and fundamental than that of cells as units (Heidenhain, 1907). We have accordingly regarded cells not as elementary organisms primarily responsible for the development and evolution of the Metazoa and Metaphyta, but as subordinate parts of varying morphological rank which are results, rather than causes, of organization. Although we thus look upon cellular organization as initially a result of differentiation, it is also true that it has, in turn, conditioned differentiation of a higher degree. The presence of cell partitions allows a more effective segregation of functionally specialized regions, and a fuller play to those important physico-chemical processes which depend on surfaces and thin films for their action. The evolution of higher organisms has unquestionably been very largely conditioned by the multicellular state, but we should think of them primarily as highly differentiated protoplasmic individuals rather than cell republics.

Considerations of phylogeny do not lie within the scope of this book, but we have taken occasion to point out the phylogenetic corollaries of the Cell and Organismal Theories. The conjectural nature of such speculations must be borne in mind. Our knowledge of many important features of the life cycles of Protista is so meager (see Kofoid, 1923), and our conceptions of the significance of structural and functional resemblances are so subject to change, that no more than provisional hypotheses regarding relationship are warranted. There is much to be said in support of Dobell's (1911) protest against the use of such admittedly convenient expressions as "primitive and advanced," "simple and complex," "lower and higher" with reference to unicellular and multicellular organisms. These terms have a subjective origin, whereas all we know objectively is that the two general classes of organisms have evolved in different ways.

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# CHAPTER IV

## THE NUCLEUS

It is now a half-century since a new era in cytology was ushered in by a series of researches revealing the remarkable behavior of the nucleus during the critical stages of the life cycle. Because of the peculiarly intimate relation which this behavior has been shown to bear to many outstanding biological problems, particularly that of heredity, it is largely in nuclear phenomena that cytological interest has continued to center up to the present day. The most striking of these phenomena form the subjects of several subsequent chapters; at this point the nucleus will be considered only as it appears in the "metabolic" or "resting" condition, *i.e.*, when not undergoing division.

Whether or not one shall say that all protoplasm or all cells are nucleated will depend upon what is meant by the term nucleus. If the chromatic substance, no matter whether distributed throughout the cell in the form of granules or aggregated to form a well-defined organ, be regarded as constituting a nucleus, then it follows that with very rare exceptions (p. 81) all plant and animal cells normally have nuclei. If, however, as certain protozoölogists prefer, the term "nucleus" be employed only with reference to a distinctly delimited organ, we must regard those Protista with scattered chromatic material as devoid of nuclei, although they possess material which performs at least the nutritive functions of a nucleus. In nearly all known organisms there are nuclei with roughly the same general type of organization, which indicates that the functional or structural differentiation of protoplasm into cytoplasm and nucleus must have occurred at a very early period in the history of the organic kingdoms.[1]

**General Characters of Nuclei.**—The number of nuclei present in any mass of protoplasm depends primarily on the bulk of the mass, since within limits a certain ratio of nuclear surface to cytoplasmic volume must be maintained for the proper action of the system as a whole. A small mass with but one or a very few nuclei may grow into an extensive cœnocytic body with thousands of nuclei produced by repeated division, as in the Siphonales and Phycomycetes. In such a body a few partitions may be formed, giving cells with varying numbers of nuclei, as in *Cladophora* (Fig. 8, *C*). Again, the subdivision into cells may be very closely correlated with the division of the nuclei, so that every cell has one nucleus; this is the condition in the majority of organisms. Frequently, cells with two or more nuclei occur regularly in certain tissues of plants with uninucleate cells elsewhere throughout the body, as in the internodal cells of Characeæ, tapetal cells, and a number of other instances in vascular plants (Arber, 1920).[1] A peculiar condition is found in the red blood corpuscles of mammals and amphibians. These cells are originally nucleated, and the later enucleate condition has usually been attributed to an actual loss or degeneration of the nucleus. In amphibians, however, Beyer (1921) and Emmel (1924) find that the enucleate erythrocyte ("erythroplastid") arises by the division of a nucleated cell without an accompanying nuclear division. Emmel (1925) reports the presence of enucleate leucocytic elements also.

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[1] For an exhaustive review of the literature on plant nuclei, see Tischler (1921–1922, especially Chaps. 1–4). Von Neuenstein (1914) gives a systematic account of alga nuclei. Agar's (1920) book on Cytology is chiefly an account of the structure and behavior of the metazoan nucleus.

In certain infusoria two kinds of nuclei are regularly present. In *Paramœcium caudatum*, for example (Fig. 22), there is one small micronucleus which divides by a peculiar form of mitosis, and one large meganucleus (macronucleus) which divides amitotically. An amicronucleate race is known in this species (Landis, 1920) and in a number of others (Woodruff, 1921). In some species there may be more than one micronucleus. The meganucleus appears to be primarily a special nutritive organ, showing decided alterations under changing environmental conditions (Stolte, 1922). At certain intervals it is absorbed completely and replaced by a new one derived by a process of division from the micronucleus, the latter continuing from generation to generation as a kind of reserve. At the time of conjugation both this replacement process (endomixis) and an exchange of parts of the micronuclei of the conjugants take place (Woodruff and Erdmann, 1914). C. V. Taylor (1923*a*), working with *Euplotes*, observed that individuals from which the micronuclei had been artificially removed underwent only one or two more fissions and died in a few days.[2]

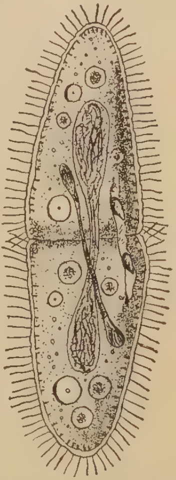

FIG. 22.—*Paramœcium caudatum* undergoing fission; mega- and micronuclei dividing. (*From Minchin, after Bütschli and Schewiakoff.*)

The position of the nucleus is determined largely by physical causes, such as surface tension, the position of the vacuoles, and the relative density of the cytoplasm in different portions of the cell. In a nonvacuolated cell it ordinarily occupies the center of the cytoplasmic mass, whereas in a cell with vacuoles it is imbedded in the cytoplasm even when the latter is reduced to a thin parietal layer; it never lies free in the vacuole. In the Cladophoraceæ it is regularly imbedded, at least partially, in the chloroplast (Carter, 1919). Its position is also related to the functions of the cell; generally speaking, it lies in the region characterized by the most active metabolism. For example, in young growing root hairs (Fig. 23, *B*) and pollen tubes it is commonly found a short distance from the elongating tip. Thus Wendel (1918) observed that the root hairs of *Sinapis alba* seedlings grow first at the apex, then at the base, and sometimes at the apex once more, and that the position of the nucleus changes accordingly. In *Tradescantia*, Farr (1925) finds no relationship between the position of the nucleus and the rate of elongation. In thickening epidermal cells (Fig. 23, *A*) it frequently, though not always, lies near the wall upon which the thickening material is being deposited. This relation of position to function was emphasized in the works of Haberlandt (1887) and Gerassimow (1890, 1899, 1901).

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[1] A historical review of known cases is given by Beer and Arber (1920). See also Tischler (1921–1922, pp. 212 ff.).

[2] For certain theories involving the micronucleus and meganucleus, see pp. 236 and 344.

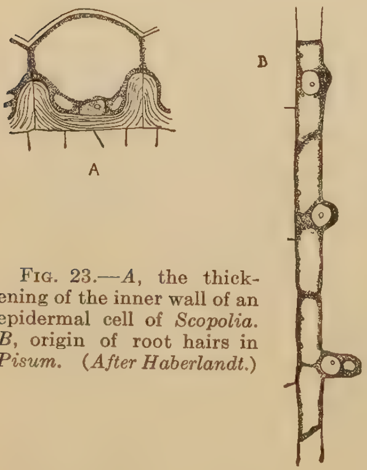

Fig. 23.—*A*, the thickening of the inner wall of an epidermal cell of *Scopolia*. *B*, origin of root hairs in *Pisum*. (*After Haberlandt.*)

In form the nucleus is typically spherical or ellipsoidal, its shape, like its position, being determined by a number of physical factors. Under comparatively uniform conditions, such as obtain where a small nucleus lies in a relatively large amount of nonvacuolated cytoplasm, a spherical shape is assumed as a result of surface tension. Exceptions are often seen in cells with specialized functions. In the cells of the spinning glands of *Pieris* and *Vanessa* (butterflies) the physiological conditions lead to the assumption of very irregular forms whereby the nuclear surface is considerably increased (Fig. 24, *A*). Nuclei seem rather commonly to undergo amœboid changes in shape; such active movement can be directly observed in the nucleus of the living cycad spermatozoid. In the long, narrow cells of vascular bundles the nuclei, which are not free to grow in all directions, come to be correspondingly elongated. The nucleus may also be passively forced into very irregular shapes by the accumulation of starch grains and the diminution in the amount of cytoplasm, as in the endosperm cells of maize. In *Stentor* and *Spirostomum* the nucleus has the form of a string of beads (Fig. 24, *B*).[1]

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[1] A discussion of the various factors influencing nuclear shape is given by Champy and Carleton (1921). Tischler (1921–1922) describes many unusual forms of nuclei, and gives a long list of measurements of plant nuclei.

With respect to the physical nature of the nucleus as a whole, the researches of Kite (1913) and Chambers (1914, 1917, 1921) have shown that it ordinarily consists, at least in part, of a gel having a higher viscosity than that of the cytoplasm, often being so firm that it can easily be handled without injury by means of the dissecting instrument. This obviously would be impossible were the nucleus merely a watery droplet or vesicle in the cytoplasm. The germinal vesicle (nucleus) of certain animal eggs Chambers finds to be a sol droplet with a gel membrane; when pinched in two by the dissecting instrument the two halves will reunite if they come in contact.

The chemical nature of the nucleus has been dealt with in Chapter II. With regard to its electrical properties, the nucleus is apparently negative to the cytoplasm. R. S. Lillie (1903) found that free nuclei and the heads of spermatozoa, which are almost entirely nuclear material, pass to the anode in an isotonic cane sugar solution; whereas cells rich in cytoplasm, such as large leucocytes, pass to the cathode. These results have been confirmed by Hardy (1913). The difference in electrical potential on the two sides of the nuclear membrane may be of considerable significance in the life processes. Most investigators have found that vital dyes do not stain the nucleus as long as it is in the living condition, but P. Dangeard (1923*a*) reports that nuclei in certain cells with a somewhat retarded activity (pollen grains of gymnosperms; endosperm of *Ricinus*) may be so stained with neutral red, methyl violet, and Dahlia violet.

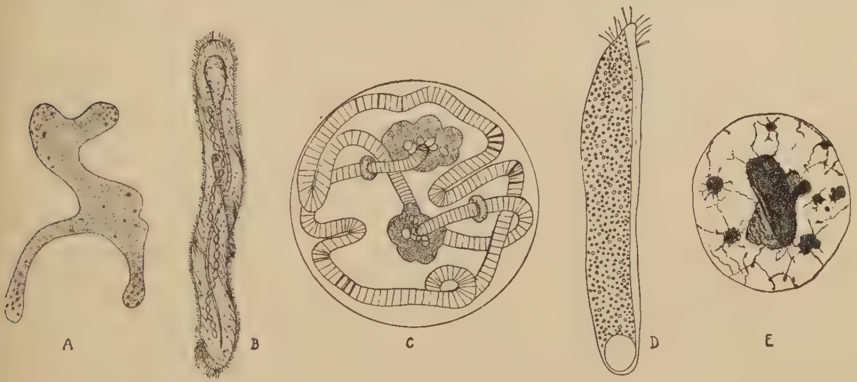

FIG. 24.—Unusual types of nuclei.

*A*, portion of nucleus from spinning gland of *Vanessa urticæ*. (*After Korschelt*, 1896.) *B*, *Spirostomum ambiguum*, with moniliform nucleus. (*After Stein*.) *C*, Nucleus from salivary gland of *Chironomus:* the chromatic material exists as a series of discs in a convoluted thread, which ends in two nucleoli. (*After Balbiani*, 1881. *See also van Herwerden*, 1910, 1911; *Alvaredes*, 1912; *Faussek*, 1913; *Tänzer*, 1921.) *D*, *Chænia teres*, with chromatic granules scattered throughout the body. (*After Gruber*, 1884). *E*, Nucleus from root tip of *Marsilia*, showing concentration of chromatic material in the nucleolus. (*After Berghs*, 1909.)

In size nuclei show very wide variation, ranging in plants from the extremely minute nucleus of *Mucor*, 1μ or less in diameter, to the relatively gigantic nucleus of the *Dioön* egg, with a diameter of 600μ. A similar range is seen in animal nuclei. Although the nuclei of the fungi are characterized by small size, most of them being less than 5μ in diameter, they may grow to be very large at certain stages. The primary nucleus of *Synchytrium*, for instance, reaches a diameter of over 60μ. The majority of nuclei, however, fall between 5 and 25μ. In spite of the wide range in the size of nuclei of different organisms, it is generally uniform in a given tissue, though it may vary considerably with the physiological activity (Maige, 1923).

*Nucleoplasmic Ratio.*—Of more importance than the absolute size of the nucleus is the relation of its volume to that of the cytoplasm—the so-called karyoplasmic or nucleoplasmic ratio. Many years ago it was held by Sachs (1892, 1893, 1895) and Strasburger (1893) that the size of a meristematic plant cell maintains a very definite relation to the size of the nucleus, owing to a supposed limitation of the sphere of influence of the nucleus. This conception has recently been emphasized anew by Winkler (1916), and parallel views have been expressed by several zoölogists.[1] In the case of certain terminal meristems of plants such a rule may well hold true within limits, but the condition reported by Bailey (1920) in the lateral meristem (cambium) shows clearly that it cannot have universal application. The cambial initials may vary enormously in size with no corresponding variation in the size of their nuclei; two such initials, one of them having many hundreds of times the volume of the other, may possess nuclei of approximately equal size. Tischler (1924) connects the ratio in pollen with the process of germination.

The nucleoplasmic ratio has figured prominently in discussions of the problem of senescence. R. Hertwig in 1889 advanced the theory that physiological depression, senescence, and natural death are associated with an increase in the relative size of the nucleus. He later asserted (1903, 1904, 1908) that the nucleoplasmic ratio is self-regulatory within certain limits for each kind of cell, the proper equilibrium disturbed by growth and differentiation being restored by certain processes, notably cell-division and extrusion of nuclear material, which are thus in a sense under the control of the ratio. Such a relation of nucleoplasmic ratio to differentiation was reported by Popoff (1907) for sex cells, Marcus (1908) for thymus cells, and Howard (1910) and Howard and Schultz (1910) for tumor cells. Minot (1891, 1908, 1913), on the contrary, believed an increase in the relative volume of the cytoplasm, in addition to its differentiation, to be a fundamental factor in senescence and death. Conklin (1912), as a result of his work on *Crepidula*, denied the existence of a constant and self-regulatory nucleoplasmic ratio, holding rather that changes in this ratio are not causes of such cell activities as cell-division, but results of the metabolic processes by which such cell activities are brought about. If the amount of interchange between nucleus and cytoplasm decreases, senescence occurs, while an increase is accompanied by rejuvenescence. In general, however, the nuclei are relatively largest in the least differentiated cells. Child (1915) points out that in most animal tissues there is an increase in the relative amount of cytoplasm during senescence, whereas in plants, although the cell enlarges through vacuolation, the relative volume of cytoplasm often does not increase. He therefore concludes that the nucleoplasmic ratio cannot be regarded as a universal factor in senescence; it is rather an indication of the kind and rate of metabolism. The differentiation of the cytoplasm, apart from its mere change in volume, Child, with many other workers (Minot, Delage, Jennings, etc.), regards as a matter of the greatest importance in senescence.

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[1] Dolley (1913) on nerve cells; Hegner (1919) on *Arcella;* Hegner and Wu (1921) on *Opalina;* Dolley (1925) on pancreatic cells.

Not only has it been held that there is a certain relation between the mass of the nucleus and that of the cytoplasm, whatever the significance of this relation may be, but there also seems to be a relation between the size of the nucleus and the number of chromosomes. In 1895 Boveri showed that the size of the nuclei in merogonic echinoderm larvæ (see p. 414) is dependent upon the number of chromosomes each contains. In a more extended study (1905) he demonstrated that it is the surface of the nucleus that is proportional to the chromosome number, and also that the size of the cell is proportional to both. Gates (1909), however, adduced evidence to show that this rule is by no means universal. This question has been investigated in connection with studies on apogamous plants and polyploid mutants, with the general result that, although in the majority of cases a rise in the chromosome number is seen to be accompanied by an increase in nuclear and cell size, there are a few cases in which it is accompanied rather by a decrease in the size of the chromosomes. This indicates that it is volume of karyotin, and not mere number of chromosomes, that is of importance in this connection (see Tischler, 1921–1922, pp. 588ff.).

**Structure of the Nucleus.**—Since the structure of the typical nucleus is a matter of such fundamental importance, it is especially unfortunate that so many points are still subject to controversy.

The nucleus is bounded by a distinct *nuclear membrane* ("karyotheca," Lundegårdh, 1912). A number of early observers denied the existence of a membrane, thinking rather that there was merely a line of contact between the nucleus and cytoplasm which might be rendered more distinct by an accumulation of chromatic matter near the boundary; and more recently some have held that the fundamental basis of both regions is continuous, no actual membrane being present between them

(Stauffacher, 1910, 1911; von Derschau, 1911, 1915). What is now known of the physical properties of both ordinary and colloidal fluids makes it seem necessary that a distinct structural alteration of some kind must be present at the nucleo-cytoplasmic interface. It has been suggested[1] that the membrane is a denser zone of cytoplasm, somewhat like the albumin membrane about an ether droplet suspended in albumin. An actual membrane or "surface film" may develop between two fluids which do not undergo chemical interaction, and if such interaction does occur a chemically distinct precipitation membrane may result. Nuclear membranes have been likened to both of these kinds of films, which may be rendered more conspicuous by the coagulating effect of fixing reagents. Another interpretation is that the nuclear boundary is, at least in part, made up of the outer surfaces of the chromosomes (Robyns, 1924). These views will be mentioned again in connection with nuclear division.

The researches on living cells by Kite, Chambers, C. V. Taylor, Gross, and others leave no doubt that the membrane is a distinct morphological structure. It is evident that in many cases it is extremely thin—1μ in *Aloë* according to Molisch (1899); and it has even been suggested that it may sometimes be but one molecule thick. In most cells under the microdissection instrument, however, it appears to be thicker, remaining intact when the nucleus is pushed and pulled about or removed from the cytoplasm, and being thrown into folds when the fluid within is withdrawn with a pipette. Andrews (1915) observed that a hole remained in the membrane after the nucleolus had been thrown out by centrifuging. The nuclear membrane is a real structure, but its origin and exact nature have not yet been fully determined.

The bulk of the nucleus is composed of a highly transparent ground substance known as *karyolymph*, or *nuclear sap*. This usually appears perfectly homogeneous, with at most but a few dispersed particles, though some have claimed that it is made up of large, pale "œdamatin granules" (Reinke, 1894; Maziarski, 1910). Microdissection (Chambers) and the Brownian movement of the suspended particles (Gross) show that it may be in either the sol or the gel state. In old cells vacuoles may appear in the karyolymph (Kisser, 1922). The origin of the karyolymph and its relation to other protoplasmic substances, particularly the nuclear reticulum, are both very obscure points. The most prevalent opinions are that it enters the nucleus at the close of mitosis, probably being continuous with the karyolymph of the mother nucleus, (Strasburger, de Litardière), and that it is derived periodically from the chromosome substance (Tischler and others).

Imbedded in the karyolymph is another component which usually has the form of a more or less continuous network, and which is therefore called the *nuclear reticulum*. This reticulum was seen in living cells of

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[1] Strasburger, Lawson (1903), de Litardière (1921*b*).

*Allium* and *Vicia* by Lundegårdh (1912*a*), in *Amœba* by Kite (1913), and in ferns by de Litardière (1921*b*). Most recent observers report that in both bright and dark-field the nucleus if uninjured shows no internal structure except the nucleolus, and that the reticulum gradually appears as the nucleus becomes moribund as the result of experimental injury (Lewis and Lewis, 1924; Chambers, 1924). In view of the results obtained by Chambers with spermatocytes, the most probable interpretation of this fact is not that the reticulum is actually formed anew, but that by some change in refractive index or other alteration it is rendered more visible. Its close physical similarity to the karyolymph is further indicated by the fact that it offers no special resistance to the passage of the microdissection needle through the nucleus, and also by the failure of a displaced nucleolus to return to its former position when released (Chambers). The general appearance of the reticulum—its coarseness and degree of continuity—depends largely upon the ratio of its volume to that of the karyolymph, as in a two-phase colloidal system (Fig. 2). O. Hartmann (1919) found the coarseness to vary with the temperature.

After many years of research comparatively little is known about the finer constitution of the nuclear reticulum. For a long period the prevalent view was that it comprised two distinct elements: a supporting framework composed of *achromatin* (Flemming, 1879), or *linin* (Schwarz, 1887), upon or in which was carried a second highly stainable substance, *chromatin* (Flemming, 1879), in the form of granules or fluid droplets. Moreover, Heidenhain (1894) distinguished two kinds of chromatin granules in the linin support: *oxychromatin* and *basichromatin*.[1] These are colored by acid and by basic dyes respectively, and can change into one another by the addition and loss of phosphorous, which accounts for the cyclic alteration in staining reaction observed during each nuclear division. They also differ in solubility (Oes, 1908, 1910; Němec, 1909, 1910).

This conception of nuclear structure has been much criticized. In the first place, the existence of two distinct kinds of chromatin is very doubtful. It now seems preferable to regard oxychromatin and basichromatin as varying and intergrading states of one complex substance, chromatin. As Lundegårdh (1910) and McClung (1924) have emphasized, the changes in staining reaction are strictly correlated with changes in the physical condition of the chromatin; in the diffused condition (reticulum) it stains as oxychromatin, and in the condensed condition (formed chromosomes) as basichromatin. This recalls A. Fischer's 1899 discovery that the staining reactions of protein particles depend in part upon their size, and thus diminishes the apparent need of chemical differences to explain all alterations in the stainability of chromatin. The physical variations are undoubtedly accompanied by certain variations in chemical composition, but at present the evidence favors the view that oxychromatin and basichromatin are not two distinct substances, but two "functional states" of one (Stieve, 1921).

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[1] See the discussion by Stieve (1921). As used by many writers the term "oxychromatin" includes also the linin, "chromatin" denoting only the basichromatin. Heidenhain later called the chromatin granules "chromioles," a term introduced by Eisen (1899).

There is also a growing tendency to apply a similar interpretation to the relation between chromatin and linin. In a large number of investigations no evidence has been found for the existence of two morphologically distinct elements in the reticulum, the latter appearing rather as one substance whose staining reactions in different regions are dependent on the degree of physical dispersion. Consequently, if there are two elements, chromatin and linin, in the reticulum they are not morphologically distinct, but chromatin must exist in the form of a thin fluid which flows freely through the linin substratum.[1] Or, it may be that the respective strong and weak staining reactions of coarser and thinner portions of the reticulum are due not to the presence and absence of a special chromatic component, but rather to differences in the actual volume and degree of condensation of a single reticular substance in these regions. This interpretation has been emphasized anew by McClung (1924). Although the staining and non-staining regions are rather sharply delimited at times, as in the course of mitosis (Chapter IX), many workers have found that all purposes of description are served by the conception of a reticulum composed of a single substance which stains variously according to its physio-chemical state in different regions and at different stages of the nuclear cycle. This one substance is commonly spoken of as chromatin, but because of the long application of this term to a supposedly distinct component of the reticulum, it is advisable to use Lundegårdh's (1910) term *karyotin* for the reticular substance as a whole. Only future research can decide whether karyotin ("chromatin" in the wide sense) is a true chemical compound or a looser combination of two or more constituents, only one of which is "chromatin" (in the narrow sense).

With regard to the chromosomes into which the nuclear material transforms at the time of nuclear division, it has been held by most of the investigators whose works are cited above that they are derived wholly from the karyotin reticulum, which therefore represents the chromosomes in the metabolic stage. Certain writers, however, have found grounds for the view that some at least of the hyaline non-reticular constituent of the nucleus must belong to the chromosomes. Thus Martens (1922) states that in *Paris quadrifolia* the chromosome is at all stages composed of two morphologically distinct elements, one of which forms the chromatic reticulum, while the other is an achromatic matrix which has been confused with the karyolymph. Some have even thought that the karyolymph itself is chromosomal, at least in origin, and that the nucleus is therefore composed solely of chromosomes. These points, which are obscure but very important, can be more profitably discussed in connection with mitosis, in Chapter IX. One may here be warned against confusing this non-reticular achromatic matrix with the supposed achromatic constituent ("linin") of the reticulum.

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[1] Grégoire and Wygaerts (1903), Grégoire (1906), Sypkens (1904), Martins-Mano (1904), Malte (1910), Lundegårdh (1910, 1912), Tischler (1915), Sharp (1913, 1920), de Litardière (1921*b*).

In many nuclei there are at certain stages one or more conspicuous accumulations of karyotin at certain points in the reticulum. Of the many terms applied to these the most suitable seems to be *chromocenters* (Baccarini, 1908).[1] After certain stains (iron-alum-hæmatoxylin) they may at times closely resemble true nucleoli, but the distinctness of the two was long ago demonstrated with other stains (Rosen, 1892). Although they are essentially masses of karyotin, perhaps newly elaborated, there are indications that they may differ somewhat in chemical composition from the rest of the reticulum (Gross, 1916). In general, it seems that their material is used in forming the chromosomes and is thus distributed to the daughter nuclei in mitosis, but in certain ferns de Litardière (1921*b*) finds that they pass into the cytoplasm.

**The Nucleolus.**—Nearly all nuclei contain one or more *true nucleoli*, or *plasmosomes* (Ogata, 1883).[2] The number is usually very small, a single one being most commonly found, but in certain tissues higher numbers may be regularly present. They seem to be absent from male gametes as a general rule. In the living nucleus the nucleolus appears as a dull, viscous droplet, usually round but frequently irregular in shape. Centrifuging shows it to be heavier than the rest of the nuclear substance.[3] It may be homogeneous throughout, or it may contain vacuoles, in which there are occasionally small granules variously known as "nucleolini" or "argentophile granules."[4] The outer dense envelope frequently observed in fixed preparations is at least in many cases an artifact. Likewise the clear area seen about the nucleolus and the strands connecting the latter with the reticulum are often, but apparently not always, to be interpreted in the same way. Chemically, the nucleolus is composed mainly of proteinaceous materials.[1] It usually shows an affinity for acid dyes, but it may become decidedly basichromatic at certain periods (see Jörgensen, 1913*a*). Its reaction in this respect is often attributed to the transfer of chromatic fluid to and from the reticulum. According to de Litardière (1925), alterations caused by heat indicate that the nucleolus in the *Allium* root is composed of an achromatic substratum which is impregnated by a less resistant chromatic substance. Certain peculiar nucleoli appear to be made up of two distinct parts differing in their staining reactions; such "amphinucleoli" or "paranucleoli" are not well understood.[2]

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[1] They have been variously known as *net knots* (Flemming, 1882), *karyosomes* (Ogata, 1883), *pseudonucleoli* (Rosen, 1892), *Nebennucleoli* (Zacharias, 1895), and *chromatin nucleoli*. *Karyosome* is the term most widely adopted (it was used in the first edition of this book), but the fact that it has been applied to other quite different elements has made the substitution of another term advisable. Tischler (1921–1922) also prefers *chromocenter*.

[2] For general accounts of the nucleolus and reviews of the literature pertaining to it, see Montgomery (1899), Wager (1904), M. Jörgensen (1913*a*), A. Meyer (1917, 1920) Tischler (1921–1922), Ludford (1922).

[3] Mottier (1899), F. M. Andrews (1903), E. W. Schmidt (1914).

[4] Digby (1910), Reed (1914), Kuwada (1919), Carleton (1920), Saguchi (1920*b*).

The origin and the growth of the nucleolus and its behavior at the time of nuclear division can be discussed in detail only after mitosis has been fully described (Chapters IX and XII). The principal difficulty lies in determining the relation of the nucleolar material to the karyotin throughout the various phases of division. The nucleolus commonly disappears as the chromosomes form and reappears in the new nuclei at the close of mitosis. This, together with other facts which will be mentioned later, has led to the view that the two nuclear elements have a close functional relationship. Kossel suggested that the albuminous nucleolar material arises as one of the products formed when complex albumin-rich compounds are split to form albumin-poor "chromatin." Nucleoli are frequently seen to fuse, and they may also be passively divided. They were supposed by Montgomery (1899) and Buchner (1910*a*) to grow by the addition of material arising outside the nucleus, but the evidence for this view is regarded as inadequate by Jörgensen (1913*a*). In certain thallophytes and Protozoa the peculiar nucleoli may undergo a regular fission as the nucleus divides (Chapter XII).

Various opinions have been expressed regarding the function of the nucleolus. It was generally looked upon by the earlier workers as a protoplasmic organ of a special type.[3] More recently, however, the tendency has been to regard it rather as an accumulation of albuminous materials of uncertain function. Haecker (1895, 1899*a*) thought it a useless by-product, but few have agreed with him. The more general tendency has been to see in the nucleolar material a reserve product of metabolic activity, perhaps in part continuous from generation to generation, this product being used in the upbuilding of one or another of the constituents of the protoplast. Although it has been thought to be a reserve for the achromatic figure,[4] or for the cytoplasm (Stieve, 1921), most workers have inclined to the view that it is the chromosomes especially which make use of the nucleolar matter.[1]

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[1] Zacharias, A. Meyer, Unna and Fein (1921).

[2] See Obst (1899), Rohde (1903), M. Jörgensen (1913*a*), Modlewski (1918).

[3] Flemming (1882), Zacharias (1885), A. Zimmermann (1887, 1893), Leydig (1885), Rohde (1903).

[4] Strasburger (1895–1907), Swingle (1897), Fairchild (1897), Němec (1910).

Mention should be made of the view that certain animal nucleoli are in some way concerned in the elaboration of secretion and storage products. In growing eggs, for example, it has been stated that nucleolar material is extruded into the cytoplasm, where it contributes to the formation of yolk or other energy-yielding products.[2] In the cells of the pancreas nucleolar matter is reported to function in a similar manner in the elaboration of zymogen (Macallum, 1891; Saguchi, 1920). The secretions of the silk glands of certain insects have been attributed in part to nucleolar extrusions by Maziarski (1911) and Nakahara (1917, 1918*a*). Ludford suggests that the nucleolus may be enzymatic in nature. Both Saguchi and von Derschau (1914) regarded the extruded nucleolar particles as chondriosomes. Although it is not improbable that the processes through which secretion and storage products are built up in some way involves nucleolar activity, the evidence for the actual passage of granules or globules through the nuclear membrane is not adequate, and the view that nucleolar matter becomes yolk has been adversely criticized (M. Jörgensen, 1913*a*; A. Meyer, 1917, 1920). Jörgensen shows that the supposed nucleolar matter in the cytoplasm is another unrelated ergastic substance.

Both Jörgensen (1913*b*) and Meyer (1917, 1920), who have made exhaustive studies on nucleoli, question the value of most of the hypotheses of specific nucleolar function; and although they are convinced that the nucleolar reserve is in some way utilized by the protoplast, they are unable to state in what manner or by what organs this is accomplished. Meyer cites as evidence favoring its ergastic reserve nature the fact that it decreases in size and may disappear in endosperm cells during the early stages of germination, in vessels as they form their wall thickenings (Kiehn, 1917), in living cells of a dying leaf, in the formation of male gametes, and in darkness. Moreover, it enlarges as the plant enters the dormant state. Its behavior in oöcytes, spermatocytes, and other growing cells is in harmony with the view that it bears some relation to the growth of the protoplast as a whole. That it is through interactions with the karyotin that the nucleolus functions in the life processes is strongly suggested by the results of Kossel's analyses, as well as by the phenomena observed by cytologists at the time of nuclear division (Chapter IX).

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[1] Flemming (1882), Strasburger (1884), Korschelt (1884, 1891), F. M. Andrews (1901), Gardner (1901), Rhumbler (1893), R. Hertwig (1898), Lubosch (1902), Farmer (1907), Sheppard (1909), Maziarski (1910), Reed (1914), Schürhoff (1918), Digby (1919), de Litardière (1921*b*), Ludford (1922*a*), Cleland (1922, 1924), Lenoir (1922), Martens (1922), Van Camp (1924).

[2] Macallum (1891), Lubosch (1902), Rohde (1903), Ludford (1921, 1922).

**The Functions of the Nucleus.**—Many years ago Claude Bernard (1878) suggested that the nucleus is the cell organ which is most essential to synthetic metabolism. Since that time various investigators have sought to test this hypothesis by experiments on cells artificially deprived of their nuclei by means of plasmolysis, centrifuging, direct section, cooling, or anesthesia. The early experiments of Klebs (1887, 1888), Haberlandt (1887), Gerassimow (1890, etc.), and others on algæ and moss cells, which had been made to separate into nucleate and enucleate portions by the action of strong sugar solutions, seemed to show that the portions without nuclei were able to form no cellulose membranes and in certain cases (*Œdogonium*, *Funaria*) no starch, though they might grow a little, use up their starch reserve to some degree, and live for a considerable length of time. Recently Haberlandt (1919, 1921) reported that starch is not used up in enucleated cells of *Elodea* and *Pelargonium.* Heitz (1922) observed that plastids fail to divide in enucleated portions of moss cells, while they continue to divide actively in the nucleated portions. The above conclusion regarding cellulose membranes was contradicted by Palla (1889, 1890) and Acqua (1891), who found that such membranes are developed by enucleated portions of pollen tubes, root hairs, and rhizoids. Townsend (1897) reported that such portions form membranes only when they remain connected by cytoplasmic strands with nucleated portions, but Palla (1906), Acqua (1910), and Bobilioff-Preisser (1917) later showed that such connections are not necessary. These results, together with those of van Wisselingh (1909) on centrifuged cells of *Spirogyra*, lead to the general conclusions that such activities as the formation of cellulose membranes, assimiliation, the utilization of reserves, and growth depend upon the presence of specific substances (building materials, enzymes, etc.) in the cytoplasm; that such substances are elaborated with the coöperation of the nucleus; and that the occurrence or non-occurrence of the activities in question in enucleated masses of cytoplasm depends upon the presence or absence of these products of previous nuclear reaction (Tischler, 1921–1922).

Noteworthy in this connection are certain experiments on amœbæ, which can be cut into nucleate and enucleate pieces. Štolc (1910) and Lynch (1919) have shown that enucleate pieces may move, respire, and respond to stimuli—activities which depend upon catabolic processes. But they do not undergo regeneration, growth through the formation of new albuminous material, or division—activities that involve organic synthesis. Of equal interest are similar experiments that have been carried out with *Stentor*, which has a nucleus like a string of beads. Gruber (1885) and F. R. Lillie (1896) found that any fragment containing a portion of the nucleus had the power of developing into a complete individual by regeneration, whereas enucleate fragments, although they lived for a little time, failed to regenerate. Prowazek (1910), on the contrary, observed the development of enucleate fragments into small individuals. Thus it appears probable that in the Protozoa, as in the plants mentioned in the preceding paragraph, the occurrence of certain processes depends upon the presence of substances originally produced under nuclear influence, and that there is an "after effect" of the nucleus which must be reckoned with in dealing with enucleate fragments. Robertson (1923) thinks it probable that growth in the Protozoa is controlled by an autocatalytic substance periodically liberated from the nucleus as it divides. In any case the whole protoplasmic system, including both nucleus and cytoplasm, is in the long run necessary for continued life.

Among the many reactions involved in metabolism the most important, according to modern physiology, is oxidation, for the energy utilized by the organism is derived immediately from the union of protoplasm or of its constituent elements with oxygen. Oxidation has been called the "independent variable" (Loeb and Wasteneys, 1911) upon which the other reactions largely depend. A relation between the nucleus and oxidation and reduction has therefore been sought.

Spitze

Following the experiments of Spitzer (1897), who observed that nucleo-proteins extracted from certain animal tissues have the same oxidizing power as the tissues themselves, it was suggested by Loeb (1899) that the nucleus is the center of oxidation in the cell. Loeb pointed out that this would explain the inability of enucleated cell-fragments to undergo regeneration. This conclusion was supported by R. S. Lillie (1903), who later (1913) showed that rapid oxidation occurs both at the surface of the cell and at the surface of the nucleus, and also by Mathews (1915). Osterhout (1917) found that "injury produces in the leaf-cells of the Indian Pipe (*Monotropa uniflora*) a darkening which is due to oxidation. The oxidation is much more rapid in the nucleus than in the cytoplasm and the facts indicate that this is also the case with the oxidation of the uninjured cell." Other investigators[1] have opposed the oxidation theory. Lynch reports that enucleated amœbæ are more quickly injured by lack or excess of oxygen and by cyanide than are nucleated individuals, and concludes on the basis of Child's theory of the greater susceptibility of active metabolic regions that the nucleus is not specially concerned in oxidation, though it is necessary for synthesis.

Further evidence in support of the theory is brought forward by Chambers (1923*a*). In healthy cells (amœbæ, ciliated cells, echinoderm ~~eggs)~~ Janus green does not enter the nucleus, but as the cells become moribund the dye enters and colors the reticulum red. This probably means that the normal resistance to the penetration of the dye is lost, whereupon the reducing ability of the nucleus becomes manifest in the change of Janus green to diethylsafranin. This reducing power is lost at death.

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[1] Wherry (1913), W. Schultze (1913), Reed (1915), Lynch (1919).

The rôle of the nucleus in development and heredity, which has been a subject of so much discussion in recent years, will be dealt with in later special chapters (XVII–XXI), after nuclear division, meiosis, and syngamy have been described.

**The Nuclei of Protista.**—In the foregoing pages attention has been limited almost entirely to the nuclei of the higher plant and animal groups. The conditions found in certain Protista should now be considered very briefly. Since fuller treatment involves the phenomena of nuclear division, it has been deferred to Chapter XII.[1]

The question of the nucleus in bacteria is one that appears to be particularly difficult to settle satisfactorily. This is due not only to the minuteness of these organisms, which makes special methods necessary and observations very difficult, but also to the fact that a variety of conditions seems to be present in the group. That bacteria are devoid of nuclei has been held by several investigators, including A. Fischer (1894, 1897, 1899, 1903), who looked upon the observed granules as reserve materials rather than nuclear substance. Migula (1894, 1897, 1904) regarded the existence of nuclei in bacteria as very doubtful. The majority of workers, on the contrary, have held that a nucleus, or at least nuclear material, is present in some form. The most striking view is that which regards the whole bacterium in some cases as a naked nucleus.[2]

In many bacteria, particularly the larger forms, there is present a granular substance which has certain characteristics of karyotin, and which in some species exists as a single well-defined mass. The "central body" of the sulphur bacterium Bütschli regarded as the homologue of a nucleus, the peripheral portion of the cell being cytoplasm. Nakanishi (1901), who employed both intra-vitam methods and fixed material, reported the presence of nuclei in the vegetative cells and spores of a number of species. In a careful study of *Bacillus Bütschlii*, Schaudinn (1902) found that the scattered chromatic granules ("chromidia") present during most of the life cycle unite at certain stages to form dense masses or peculiar spiral figures. Such scattered "nuclear granules" and "spiral filament nuclei" have often been observed.[3] The nuclear nature of such structures was repeatedly denied by A. Meyer (1897, 1899, 1908, 1912), who held them to be modifications of the cytoplasm. Meyer described as the nuclei of *Bacillus Pasteurianus* and other forms certain minute refractive bodies distinguishable from fat, volutin, and glycogen by their reactions to stains and other reagents. Similar results were reported by Viehover (1913), Paravicini (1918), and others. Thus in *Bacillus megatherium*, Paravicini found a single minute nucleus in the vegetative cell and in the spore, and in *Bacterium ærogenes* six in the vegetative cell. In both cases cell-division was preceded by a division of the nuclei (Fig. 25). These interpretations have been questioned, though the behavior of the observed bodies at the time of spore-formation and their apparent division are very suggestive of their nuclear nature. The proper evaluation of the many differentiations in bacteria remains as one of the interesting problems of the future.

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[1] For more complete accounts of the nuclei of Protista, see the works of Wilson (1900), Meyer (1912, 1920), M. Hartmann (1911), Pavillard (1910), Guilliermond (1907, 1920), Dobell (1911*b*), Frost (1917), Minchin (1912), and Kirchensteins (1922).

[2] Zettnow (1891, 1897, 1899, 1908), Růžička (1908, 1909), and, in the case of small bacteria, Bütschli (1890, 1892, 1896, 1902).

[3] Schwellengrebel (1906, 1907, 1909), Guilliermond (1908, 1909), Dobell (1908, 1909, 1911*a*), Kirchensteins (1922).

A further unusual condition is found in the "karyosome nuclei" of many Protozoa and related forms. Here nearly all of the stainable nuclear substance is concentrated in a large central "karyosome." This seems to be a compound body which at certain stages separates into chromatin, nucleolar matter, and centriole, the closeness and constancy of the association of these elements varying widely in different species.

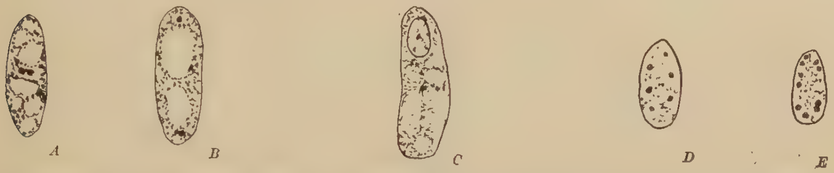

FIG. 25.—The supposed nuclei of bacteria. *A*, *B*, division of nucleus prior to fission in *Bacillus megatherium*. (*After Paravicini*, 1918.) *C*, *Bacillus Pasteurianus*, showing spore with nucleus. (*After A. Meyer*, 1912.) *D*, *E*, *Bacterium ærogenes*, showing apparent nuclear division. (*After Paravicini*.)

Such cases will be described in Chapter XII. In most Protozoa the organization of the nucleus seems to be essentially the same as that in Metazoa (Metcalf, 1915; Kofoid, 1915, 1923).

Not only in bacteria, but also in certain flagellates, Protozoa, and blue-green algæ, the chromatic material is scattered without definite limitations throughout the cell (see Figs. 24, *D* and 96, *A*). It is doubtful if such scattered granules, even if they function as "chromatin," should be spoken of collectively as a nucleus. As pointed out at the beginning of this chapter, it seems preferable to certain workers to limit the term to those chromatic aggregations which actually have the characters of a definitely localized organ. In discussing the advisability of so restricting the application of the term, Minchin (1912, Chapter VI) points out that

> . . . the word "chromatin" connotes an essentially physiological and biological conception . . . of a substance, far from uniform in its chemical nature, which has certain definite relations to the life history and vital activities of the cell. The word "nucleus," on the other hand . . . is essentially a morphological conception, as of a body, contained in the cell, which exhibits a structure and organization of a certain complexity, and in which the essential constituents, the chromatin particles, are distributed, lodged, and maintained, in the midst of

achromatinic elements which exhibit an organized arrangement, variable in different species, but more or less constant in the corresponding phases of the same species.

According to this interpretation, the term "nucleus" would not be applicable to a lot of granules (chromidia) scattered throughout the cell. Minchin states further that

> . . . as soon as a mass or a number of particles of chromatin begin to concentrate and separate themselves from the surrounding protoplasm, with formation of distinct nuclear sap and appearance of achromatinic supporting elements, we have the beginning at least of that definite organization and structural complexity which is the criterion of a nucleus as distinguished from a chromidial mass.

**Conclusion.**—In view of the striking character of the transformations undergone by the nucleus in cell-division, sporogenesis, gametogenesis, and syngamy, it is not strange that cytologists should have long devoted the major share of their attention to nuclear phenomena. Justification for this intensive study is found in the intimate relation which such phenomena bear to the important problems of development and heredity. Nevertheless, investigation of the cytoplasm and its many differentiations has been permitted to suffer from neglect; and one of the most encouraging features of present-day cytological research is the renewal of emphasis upon extra-nuclear protoplasmic activity. Although the nucleus, like each other protoplasmic organ, may be particularly concerned with one or more special functions, it is to be borne in mind that the physico-chemical system exhibiting the phenomena of metabolism, ontogenesis, and heredity is protoplasm which has become differentiated into nuclear and other elements as such functions have been more highly developed and localized. Each function, though it may be peculiarly subject to the differential influence of some one organ, is, in reality, an act of the protoplasmic system as a whole.

# CHAPTER V

## PLASTIDS

The most conspicuous cytoplasmic differentiations in plants are plastids. Cytologists have long been aware of the fact that these bodies represent regions of the protoplast which have become specialized in connection with important physiological functions; and this, together with their power of division, has given them the rank of distinct organs. Interest in plastids has recently been stimulated anew by the discovery that certain characters showing peculiar modes of inheritance are closely bound up with their behavior. Such problems are complicated by uncertainties regarding the relation of plastids to another class of bodies, namely, chondriosomes, which will form the subject of the next chapter.[1]

**General Nature and Occurrence.**—Plastids are of almost universal occurrence in the tissues of plants, where they are found in one form or another in all groups with the possible exception of bacteria, myxomycetes and certain fungi. In animals, plastid-like differentiations appear to be extremely rare. Within a single cell there may be regularly but one plastid, as in many algæ, *Anthoceros*, and the meristematic cells of *Selaginella;* or two, as in *Zygnema;* or a higher number, as in the green tissues of most higher plants. They lie imbedded in the cytoplasm and are often closely associated with the nucleus; they are never found normally in the vacuole. The positions which they assume within the cell are frequently related in a definite manner to certain external conditions. In the palisade cells of green leaves, for example, the chloroplasts are found near the upper surface if the incident light is weak; whereas they react to strong illumination by taking up less exposed positions along the lateral walls.[2] Although they may vary considerably in size, Möbius (1920) found that 75 per cent of the plastids in 215 species of plants he examined had a long diameter lying between 4 and 6$\mu$. It seems that in some cases there is a relation between the size of the plastids and that of the cells in which they lie (Gates, 1923). Plastids also vary widely in shape, as will be shown in the next section. Fine fibrils connecting the plastids with the nucleus have been frequently described. These are regarded as actual prolongations of the nucleus by Lidforss (1908, 1915), but to others it appears more likely that they are cytoplasmic differentiations (Åkermann, 1915). They are said to be well preserved by osmic acid, but not by most ordinary fixing fluids. The total plastid complement of the protoplast is called the *plastidome* by Dangeard.

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[1] For general accounts of plastids, see A. Meyer (1883), Schimper (1883, 1885), Senn (1908), and Schürhoff (1924).

[2] This topic is discussed by Schimper (1885), Haberlandt (1918), and Senn (1908).

Plastids are usually classified on the basis of the colors of their contained pigments. The arbitrary nature of such a classification is apparent when it is realized that two plastids of the same color, or with no color whatsoever, may be performing very different functions by virtue of unlike substances not visible to the eye; and, further, that the same plastid may be colorless, green, and yellow or red at different stages in its history. A separation on the basis of color, however, is very convenient, and usually does correspond to functional diversity. This is shown by the interesting fact that the thallophyte groups with different predominating pigments are characterized by different principal products of metabolic activity. In the higher plants and the grass-green algæ this product is usually starch, in the yellow-green algæ and diatoms it is oil, in the brown algæ it is pentosan, in the red algæ (Florideæ) it is Floridean starch, and in the blue-green algæ it is glycogen.

**Leucoplasts.**—All colorless plastids, regardless of their size, function, or relation to other types of plastids, are known as leucoplasts (Fig. 26). They are found commonly in meristematic tissue, and may be retained in some kinds of differentiated cells, such as the glandular hairs of *Pelargonium.* Küster (1911) states that the leucoplasts of *Orchis* are of a very fluid consistency, undergoing amœboid changes of shape and multiplying by irregular fission. Many smaller leucoplasts appear to represent juvenile stages in the development of plastids of more highly differentiated types, for under certain conditions they develop into the larger and more highly specialized leucoplasts known as *amyloplasts* (Fig. 29, *C*) and into the various kinds of chromoplasts mentioned below.

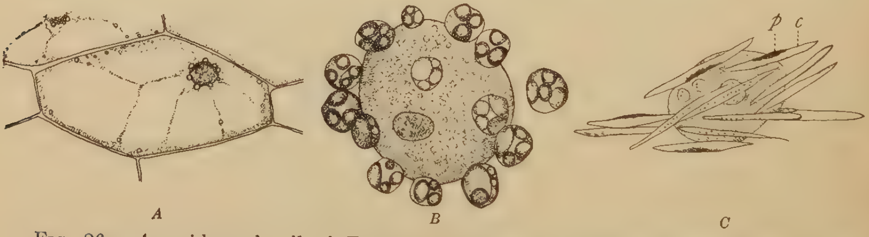

Fig. 26.—*A*, epidermal cell of *Tradescantia discolor*, with small leucoplasts. (*After Molisch*, 1913.) *B*, portion of the same more highly magnified; the leucoplasts contain albumin globules, and tend to be grouped about the nucleus. *C*, leucoplasts (*p*) with large albumin crystals (*c*) in epidermal cells of bulb of *Phajus grandifolius*. (*After Meyer*, 1883.)

**Chromoplasts.**—Chromoplasts are plastids bearing one or more pigments. They are frequently called *chromatophores*, but since this term has been used with special reference to the plastids of algæ, and also for certain pigmented cells in animals, *chromoplast* is preferable as a general term for all colored plastids. Of all chromoplasts the most familiar is the *chloroplast,* whose color is due to the presence of the green pigment, chlorophyll.

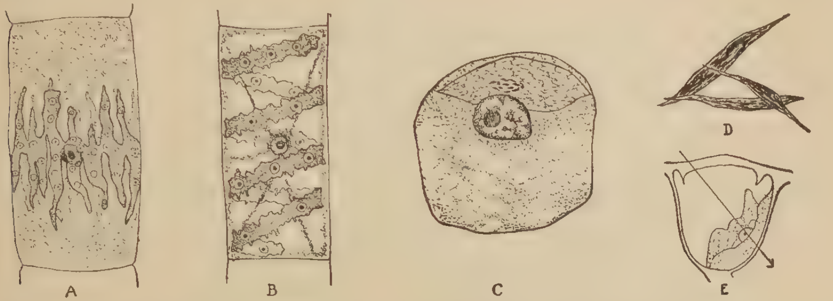

FIG. 27.—Various types of plastids. *A, Draparnaldia. B, Spirogyra. C, Anthoceros. D,* red chromoplasts of *Arisæma. E,* cell of *Selaginella,* showing position assumed by plastid in response to light (direction shown by arrow). *A, B,* and *C* show pyrenoids. (*E after Haberlandt.*)

Chloroplasts are usually spherical, ovoid, or discoid in shape, but many bizarre forms are known, particularly among the green algæ. In *Ulothrix* the plastid has the form of a complete or incomplete hollow cylinder; in *Draparnaldia* (Fig. 27, *A*), a hollow cylinder with very irregu-

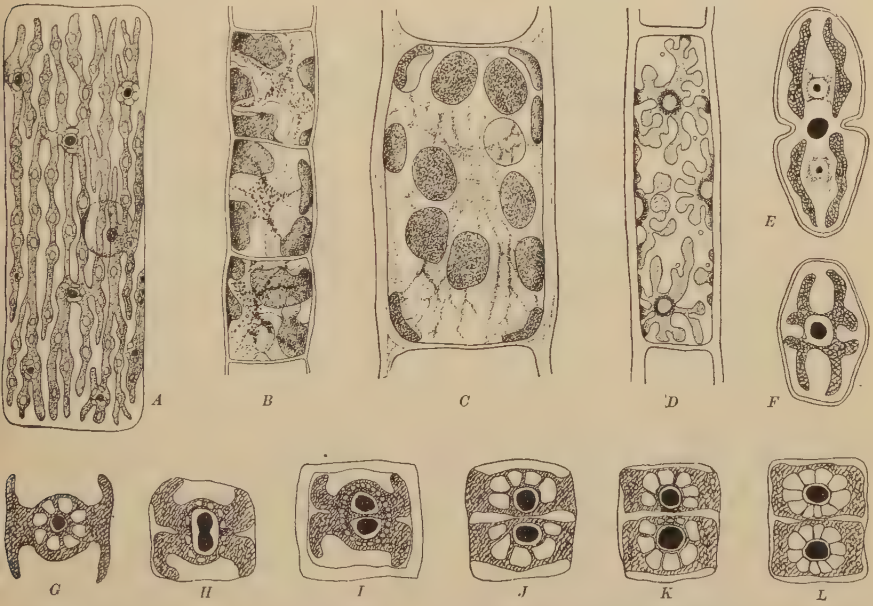

FIG. 28.—Various types of plastids. *A, Œdogonium,* showing pyrenoids and stroma starch. *B, Leptonema fasciculatum. C, Pilayella varia. D, Rhodochorton floridulum. E, F, Euastrum dubium,* front and side views. *G–L, Hyalotheca mucosa,* showing division of plastid and pyrenoid with its surrounding starch masses. (*From the works of Schmitz, Reinke, Kuckuck, and Carter.*)

lar ends; in *Œdogonium*, an irregular parietal net (Fig. 28, *A*); in *Spirogyra* (Fig. 27, *B*), a spirally coiled ribbon; and in the desmids, a series of radiating plates (Fig. 28, *E*, *F*) (Carter, 1919, 1920). The plastid of *Anthoceros* (Fig. 27, *C*) is spindle-shaped, becoming chain-like in the elongated columella cells (Scherrer, 1914). In *Selaginella* also it may thus constrict into several connected parts (Haberlandt, 1888; Emberger, 1924). The chromoplasts of *Arisæma* (Fig. 27, *D*) are frequently sharply angular, owing in part to the presence of crystals. In the Cladophoraceæ (Carter, 1919) the cell is completely lined by a thin chromatophore, which may be entire or fenestrated; in many cells irregular strands pass inward through the cell cavity. Indeed, it seems not improbable that in some cases the plastid may be not at all sharply distinct from the rest of the cytoplasm, the two grading one into the other, and the chlorophyll at certain stages permeating all parts of the cytoplasm. The observations of Timberlake and Harper appear to show that such is the condition in the young cells of *Hydrodictyon.* Thus the physiological processes show various degrees of localization, causing manifold degrees of structural transformation and delimitation of the cytoplasmic regions involved (Harper).

The most important of all plastid pigments is chlorophyll, because of its peculiar relation to the elaboration of carbohydrates by chloroplasts. Chlorophyll ordinarily develops in the plastid only in the presence of light; apparent exceptions are found in certain woods and the embryo and endosperm of certain seeds. Most young seedlings grown in the absence of light show a pale yellowish color, which is due to a substance known as chlorophyllogen in the plastids. When such "etiolated" plants are placed in the light, the plastids become green, apparently through an alteration of the chlorophyllogen to chlorophyll (Monteverde and Lubimenko, 1911). Other conditions necessary for the development of chlorophyll are a favorable temperature and the presence of iron, oxygen, and certain carbohydrates. With chlorophyll are usually associated one or both of the yellow carotinoid pigments, carotin and xanthophyll, which seem to be similar to the lipochromes of animals. There also appears to be a close chemical relationship between chlorophyll and the hæmoglobin of animal blood. The exact mutual relation of the several pigments in the chloroplast is uncertain, some investigators thinking it probable that a single green compound decomposes readily into "chlorophyll *a*," "chlorophyll *b*" and the yellow pigments when subjected to analysis (Lubimenko, 1921). In the algæ other pigments, notably brown phycophæin and fucoxanthin, red phycoerythrin, and blue phycocyanin, occur in addition to chlorophyll, though in the case of the blue-green algæ there is some question concerning the limitation of pigments to plastids (Chapter XII). The red color of tomatoes is due to the presence of lycopersicin, apparently an isomer of carotin, which is developed in the chloroplasts as the fruit ripens. The colors of flower petals are in some cases due to plastid pigments. In *Nasturtium*, for example, the yellow color is due to chromoplasts, but red pigment in the same flower is held in solution in the cell sap.[1]

The structure of the plastid and the manner in which the pigments are borne within it are extremely difficult points to determine. No limiting membrane is definitely known, but it is probable that a delicate film is present around all definitely bounded plastids. An outer envelope ("peristromium") having to do with the movement of the plastid has been described, but Fitting (1909) and Meyer (1920, 1922) interpret this as an alteration of the surrounding cytoplasm. The body of the plastid has usually been described as a finely fibrillar meshwork, the *stroma*, which may be somewhat denser toward the periphery, and in which the pigments are held as minute droplets. It seems equally probable that the stroma is homogeneous, with the droplets suspended as in an emulsion. The droplets are apparently not composed of the pigments alone, but rather of some lipoid carrying the pigments in solution. It is possible that the pigments may be in part adsorbed. Only further research can clear up these obscure points. In chromoplasts other than chloroplasts the pigments may at times assume the form of solid granules or crystals.

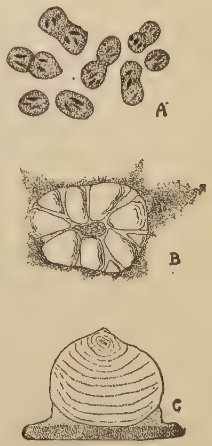

FIG. 29.—Formation of starch by plastids. *A*, dividing chloroplasts of *Funaria*, with grains of assimilation starch. (*After Strasburger.*) *B*, chloroplast of *Zygnema*, with several large starch grains about a central pyrenoid. (*After Bourquin*, 1917.) *C*, leucoplast (amyloplast) in tuber of *Phajus grandifolius*, with grain of reserve starch. (*After Strasburger.*)

**Photosynthesis.**—Of all chromoplasts the chloroplasts stand first in importance, for by virtue of their chlorophyll they are able, in the presence of light, to decompose carbon dioxide and combine the carbon with oxygen and hydrogen obtained from water to form carbohydrates, oxygen being given off as a byproduct. Chloroplasts are the world's ultimate food producers. The carbohydrate first elaborated is presumably in solution and therefore invisible. In many plants this product either accumulates in the dissolved state or is removed from the chloroplasts as fast as it is formed. Very commonly, however, there is a temporary excess, which is deposited as minute granules of *starch* in the chloroplasts.

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[1] For accounts of plastid pigments, see the works of Palladin (1918), Onslow (1923), R. W. Thatcher (1921), Beauverie (1919), Willstätter and Stoll (1913), Jörgensen and Stiles (1917), Haas and Hill (1921, 1923), Rigg (1922), Oltmanns (1923), Palmer (1922), Fulton (1922), and Lloyd (1924). The distribution of carotin is discussed in an earlier paper by Tammes (1900). Lloyd (1924) gives particular attention to fluorescent colors.

This "assimilation starch" is therefore the first visible product of photosynthesis in most green plants; in some species the product appears to be oil. As Meyer originally showed, the starch is actually synthesized within the body of the chloroplast (Fig. 29, *A*, *B*). It is later transformed through the agency of enzymes into some soluble compound, usually a sugar; in this form it may be carried to growing regions, where, after further changes, it is built into the structure of the plant; or it may pass to storage organs where it is transformed into the ordinary "reserve starch," or "storage starch." This deposition of reserve starch is in most cases brought about through the agency of *amyloplasts*, which are leucoplasts capable of changing already elaborated organic materials, such as glucose, into starch (Fig. 29, *C*). The leucoplasts of *Conopholis americana*, a colorless parasitic angiosperm, are able to form starch from elements obtained from the host plant (Mottier, 1921).

The statement made by Schimper (1880) and Meyer (1883, 1895) that starch is always formed by plastids still holds good in its essential feature; so far as is certainly known no primary product of photosynthesis is formed in the cytoplasm apart from plastids, although in some cases, such as the young cells of *Hydrodictyon*, according to Harper, it is very difficult or even impossible to distinguish the limits of these organs. The granules of "Floridean starch" in the red algæ lie in the cytoplasm, but they begin to form at the surface of the plastid as flat plates which become cup-shaped or conical, with their flattened sides remaining in contact with the plastid as long as they continue to grow (Henckel, 1901; Kylin, 1913). Mangenot (1923*a*), however, reports that they are formed some distance away from the plastids in the species studied by him. If such is actually the case, it is highly probable that they arise through the transformation of a non-visible product (sugar?) of the photosynthetic activity of the plastids, and are not immediately built up from water and carbon dioxide. A similar interpretation may be placed upon corresponding appearances reported in higher plants. Owing to the great difficulty of determining the true cell structure of the blue-green algæ (see p. 227) it is possible to speak of plastid activity in such forms only with great reserve. If these plants are without plastids, the product of photosynthetic activity, commonly glycogen, must be elaborated in the cytoplasm without their aid. If, on the other hand, the peripheral portion of the protoplast represents a large chromatophore or cytoplasm containing minute chromatophores, the photosynthetic process, although it may result in the production of a different substance, is dependent upon the powers of definite protoplasmic organs much the same as in higher plants. Among bacteria and other Protista in which it seems more certain that plastids and the ordinary pigments are absent, widely different types of metabolism are found.

**The Pyrenoid.**—The term *pyrenoid* was applied by Schmitz (1882) to the refractive kernel-like bodies imbedded in the chromatophores of the algæ. Pyrenoids are characteristic of the Chlorophyceæ especially, being present almost universally in the members of this group. They are known in a few representatives of the Rhodophyceæ (*Nemalion* and the Bangiaceæ), but apparently do not occur in the Cyanophyceæ, Phæophyceæ, and Characeæ. A peculiar pyrenoid is present in the liverwort *Anthoceros*. The chromatophore may contain but one pyrenoid, as in *Zygnema*, or a large number, as in *Spirogyra*, *Draparnaldia*, and many other forms (Figs. 26, 27).

As held by de Bary (1858), Schmitz (1884), and Schimper (1885), the pyrenoid appears to be composed of a protein substance with a thick gelatinous consistency. When a single pyrenoid is present in the chromatophore it may multiply by fission along with the latter when the cell divides (Fig. 28, *G-L*), while in those forms possessing several pyrenoids this multiplication may be much more extensive. Also, as pointed out by Schmitz and Schimper, pyrenoids may disappear and arise *de novo* from the cytoplasm or from the plastid protoplasm. In *Tetradesmus* and *Scenedesmus*, G. M. Smith (1913, 1914) finds them arising in the cytoplasm close to the nucleus. They are also reported to arise *de novo* in *Volvox* (W. Zimmermann, 1921), and *Brachiomonas* (Hazen, 1922), and both by division and *de novo* within the plastid in *Mougeotia* (Peterschilka, 1922). In *Eudorina*, Hartmann (1921) found that in a clone with several pyrenoids these were distributed in successive cell-divisions until only one was left, after which this divided, as did the regularly single pyrenoid of another clone. In *Porphyra tenella* (Ishikawa, 1921*a*) the pyrenoid is a spherical structure enclosing fusiform bodies, and its division precedes that of the plastid.

With regard to its function, the earlier workers referred to above observed that under certain conditions the pyrenoid is closely surrounded by a mass of starch grains, and concluded that it is an organ, or portion of an organ (plastid), intimately concerned in the process of starch formation, its action being somewhat similar to that of an amyloplast. The pyrenoid, in fact, has often been likened to a leucoplast imbedded in the plastid; Wiesner, for instance, believed the pyrenoid to contain several leucoplast bodies, each of which gave rise to a starch grain. In general, more recent researches have emphasized the close association of the pyrenoid with the starch-forming process, although the precise nature of this process remains very obscure. According to Timberlake (1901) the pyrenoid in *Hydrodictyon* is differentiated from the cytoplasm and is very active in starch production, segments splitting off from its periphery and forming starch within them. In this way the entire pyrenoid may become a mass of "pyrenoid starch," as distinguished from ordinary, or "stroma starch." McAllister (1913) describes a similar splitting up of the pyrenoid to form several starch grains in *Tetraspora.* Yamanouchi (1913*a*), however, in his description of a new species of *Hydrodictyon,* states that the pyrenoids have nothing to do with starch formation. Cleland (1919) recently reports a close association of the pyrenoid of *Nemalion* with the formation of Floridean starch. Von Derschau (1910, 1915) has suggested that pyrenoids may play a rôle in albumin synthesis.

A similar diversity of opinion exists with respect to the rôle of the pyrenoid in *Zygnema.* Chmielewskij (1896), who looked upon the pyrenoid as a permanent cell organ multiplying only by division, held that starch grains arise wholly from the substance of the pyrenoid, plate-like extensions of the latter being present between and in intimate contact with the developing grains. More recently Bourquin (1917) asserts that the pyrenoid has nothing to do with the appearance of starch, the body of the chromatophore alone being concerned. She observes the starch grains appearing first near the periphery of the chromatophore entirely apart from the pyrenoid, the later formed grains differentiating in positions progressively nearer the pyrenoid (Fig. 29, *B*).

The pyrenoid of *Anthoceros* (Fig. 27, *C*) as described by McAllister (1914) is, in reality, a group of about 25 to 300 small "pyrenoid bodies" which are probably composed of a proteinaceous substance. The outermost bodies become starch, new ones apparently being formed by the fission of those lying in the midst of the group. McAllister states that no pyrenoid is visible in the young sporogenous tissue, starch being formed without its aid. Somewhat later several small bodies appear and aggregate to form the pyrenoid.

The only tentative conclusion which is justified is that the pyrenoid seems to be a region of the plastid specially differentiated in connection with some reaction involved in starch formation. However, such a relation does not require that the starch should appear in direct contact with the pyrenoid. One can scarcely give credence to the view that the albuminous pyrenoid substance transforms directly into a carbohydrate, but a physiological connection of some kind between the two classes of substances seems probable.

**Elaioplasts and Oil Bodies.**—In 1888 Wakker discovered in the cells of *Vanilla* certain plastid-like bodies to which he gave the name *elaioplasts,* since they seemed to be concerned in the elaboration of oil (Fig. 30, *A*). They were soon observed in a number of monocotyledons by A. Zimmermann (1893), Raciborski (1893), and Küster (1894), and some time later in the flower parts of a dicotyledon, *Gaillardia,* by Beer (1909*a*). Politis (1914*a*) has found them in monocotyledonous plants belonging to 19 different genera, and in five genera of dicotyledons (Malvaceæ).

There is a considerable lack of agreement in the opinions expressed on the subject of the origin and significance of elaioplasts. Wakker thought it probable that they represent metamorphosed chloroplasts, which they often closely resemble in structure (Küster); whereas Raciborski asserted that they arise as small refractive granules in the cytoplasm and multiply by budding. In the zygospores of *Sporodinia grandis* and *Phycomyces nitens* Keene (1914, 1919) reports the presence of a number of globular structures with which oil is associated from their earliest stages. These unite to form one or two large reticulate bodies which are believed to be related to the elaioplasts of higher plants. All of these investigators agree with Politis that elaioplasts are normal cell organs with a special function, namely, the formation of oily substances having a rôle in nutrition. Beer, on the contrary, states that in *Gaillardia* they are formed secondarily by the aggregation of many small degenerating plastids and plastid products at one or more points in the cell, all stages of the process being observed. Although the bodies so formed may, if green, produce starch, or, if colorless, an oily yellow pigment, Beer thinks it probable that they have no important special function in the life of the plant. Meyer (1920) and Guilliermond (1922*b*) conclude that elaioplasts are not plastids at all, but ergastic accumulations made up largely of lipoids, together with certain albuminous constituents. Mangenot (1923*b*) states that oil is formed by phæoplasts in certain brown algæ.

Closely associated with investigations on elaioplasts have been those concerned with the *oil bodies* found in the cells of many liverworts (Fig. 30, *B*). These bodies, discovered by Gottsche in 1843, were first carefully described by Pfeffer (1874). Pfeffer stated that they arise by the fusion of many minute droplets of fatty oil appearing in the cytoplasm of very young cells, and later come to lie in the cell sap; he further believed them to possess a special membrane. Wakker (1888) held them to be analogous to leucoplasts and chloroplasts, multiplying by fission at each cell-division, and pointed out that they lie in the cytoplasm rather than in the cell sap. He was inclined to view them as products of elaioplasts, which Küster (1894) supposed them to resemble in having a spongy stroma containing oil in the form of minute droplets.

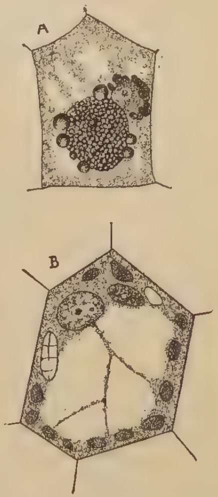

FIG. 30.—*A*, elaioplast with oil droplets in epidermal cell of perianth of *Polianthes tuberosa;* nucleus with small plastids at right. (*After Politis*, 1914.) *B*, oil bodies in various stages of development in a cell of *Calypogeia*. (*After Gargeanne*, 1903.)

Quite different were the views of Gargeanne (1903). According to him they arise from vacuoles, their limiting membranes thus being the original tonoplasts. While in the juvenile vacuole stage they may multiply by division, but when once fully formed they remain unchanged and divide no further. Gargeanne observed small oil droplets moving about freely within the oil body, and hence concluded that the latter has a fluid consistency rather than a spongy stroma as Küster thought.

The most noteworthy recent observations on oil bodies are those of Rivett (1918), who finds them to be very conspicuous in the cells of *Alicularia scolaris.* Rivett holds that they are in reality only oil vacuoles—that they originate by the coalescence of numerous minute oil droplets secreted by the protoplasm in a manner entirely similar to that in which the ordinary sap vacuole arises (*cf.* Pfeffer). Although they become very large and project well into the sap vacuole, they continue to be surrounded by a thin film of cytoplasm. The oil body, in the opinion of Rivett, is therefore in no sense a plastid, nor is it formed by any special elaioplast: it is simply an accumulation of ethereal and fatty oils together with some proteinaceous substance. The "membrane" observed by Pfeffer is the limiting layer of the surrounding cytoplasm, which may be slightly changed by contact with the oil. Meyer (1920) also shows that the oil bodies are only oily secretions which are probably of no further use, and holds the same to be true of the "elaiospheres" (Lidforss, 1893) described in the cells of various angiosperms.

**The Eyespot.**—The so-called *eyespot* present in the flagellate cell and in the zoöspores and gametes of many algæ has certain characteristics in common with plastids, and may therefore receive consideration here. This body, which nearly all workers agree is a light-sensitive organ, is an elongated or circular and flattened structure lying in the anterior region of the cell (flagellates) or near its lateral margin, usually in close association with the chromatophore and the plasma membrane.[1] With respect to its mode of origin, it has been variously reported to arise *de novo* in each newly formed zoöspore in several green algæ (Overton); to multiply by fission at the time of cell-division in flagellates (Klebs); to develop from a plastid in the antheridial cell in the case of the spermatozoid of *Fucus;*[2] and to arise as a differentiated portion of the plastid in the zoöspores and gametes of *Zanardinia* (Yamanouchi).

It is generally agreed that the eyespot in many instances consists of a finely reticulate stroma in which an oily red pigment with many of the characteristics of hæmatochrom is held in the form of minute droplets or granules[3] (Fig. 31, *C*). As shown by the careful researches of Franzé, the stroma may also bear one or more refractive inclusions, which in the Chlamydomonadaceæ and Volvocaceæ consist of starch, and in the Euglenoideæ of paramylum (Fig. 31, *D*, *E*). These inclusions were thought by Franzé to increase the sensitivity of the eyespot by concentrating the light at certain points.

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[1] E. Overton (1889), Klebs (1883, 1892), L. N. Johnson (1893), Strasburger (1900), Wollenweber (1907, 1908).

[2] Guignard (1889), Mangenot (1920*e*, 1921), Kylin (1920).

[3] Schilling (1891), Klebs (1883), Franzé (1893), Wager (1900*a*), Wollenweber (1907, 1908).

The eyespot of the zoöspore of *Cladophora* (Strasburger, 1900) appears to arise as a swelling of the ectoplast, and consists of an external pigmented layer beneath which is a lens-shaped mass of hyaline substance (Fig. 31, *B*). In *Gonium* and *Eudorina* (Mast, 1916) the lens-shaped portion lies outside with the cup-shaped opaque portion beneath it (Fig. 31, *A*), an arrangement suggesting the primitive eyes of certain animals. In neither portion has any finer structure been detected. Mast has shown that the orientation of the colony is brought about through changes in the intensity of the light falling upon the light-sensitive substance. As the unoriented swimming colony rotates on its axis, those zoöids turning away from the light have the hyaline portion of the eyespot shaded by the opaque cup; this sudden reduction in the amount of light energy received brings about an increase in the activity of the flagella of those zoöids, with the result that the colony as a whole turns more directly toward the source of light.

In *Euglena viridis* the morphological connection between the eyespot and the motor apparatus is particularly close. Here Wager (1900) has shown that the eyespot, which is a discoid protoplasmic body containing a layer of large pigment droplets, is situated at the surface bounding the œsophagus very near a swelling on one of the basal branches of the flagellum (Fig. 31, *C*).

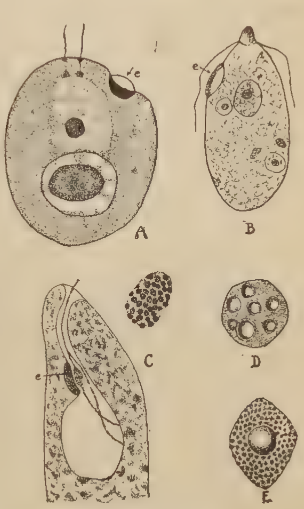

Fig. 31.—Eyespots of various types. *A*, zoöid of *Eudorina*; *e*, eyespot. (*From Mast, after Grave.*) *B*, zoöspore of *Cladophora*. (*After Strasburger*, 1900.) *C*, anterior end of *Euglena viridis*, showing eyespot at surface of œsophagus, and in front of it a swelling on one root of the flagellum; face view of eyespot at right, showing pigment granules. (*After Wager*, 1900.) *D*, eyespot of *Euglena velata*. *E*, eyespot of *Trachelomonas volvocina*, with pigment granules and crystalloid body. (*D and E after Franzé*, 1893.)

In general, it may be concluded that the eyespot in some cases bears in its structure, and to a certain extent in its evident function, such a close resemblance to the ordinary plastid that a relationship of some sort between the two seems highly probable; whereas in other cases (*Gonium, Cladophora*) it appears to represent a differentiation of the ectoplast. It is more than likely that light-sensitive organs have arisen more than once in the evolution of the lower organisms, and that they cannot all be placed in the same category.

**The Origin of Plastids.**—It was believed by the early observers, notably Schimper (1883) and Meyer (1883), that plastids never originate *de novo* but always arise from preëxisting plastids by division. Fully differentiated plastids, such as chloroplasts, can readily be seen multiplying in this manner in growing tissues with a frequency sufficient to account for the large number of plastids present in mature plant parts. Since it is known, however, that chloroplasts and other differentiated chromoplasts may arise from leucoplasts through the development of pigments and other characters in the latter, and also that the individual plant arises from gametes or a spore in which the plastids are usually in a colorless and relatively undifferentiated state, the problem of the individuality of the plastid is mainly one of determining whether these undifferentiated plastids, leucoplasts, or "plastid primordia" later developing into chloroplasts and other types are continuous through the critical stages of the life cycle, multiplying only by division, or arise *de novo* as new differentiations of the cytoplasm. Attention may first be given to certain cases in which the plastid has been followed through gametogenesis and syngamy.

In *Zygnema* (Kurssanow, 1911) each vegetative cell contains one nucleus and two plastids, all of which divide at each vegetative cell-division. In sexual reproduction the entire protoplast, with its nucelus and two plastids, passes through the conjugating tube as a "male" gamete and unites with a similar complete protoplast ("female" gamete) of another filament. The two nuclei fuse, giving the primary nucleus of the new individual (zygospore nucleus), while the two plastids contributed by the "male" gamete degenerate, leaving the two furnished by the "female" gamete as the plastids of the new individual. A similar process occurs in *Spirogyra* (Tröndle, 1911) (Fig. 104).

In *Coleochæte* (Allen, 1905) each vegetative cell and gamete has one nucleus and one plastid; after the sexual union of the gamete nuclei the zygote therefore contains one nucleus and two plastids. These two plastids divide at the first division of the zygote but not at the second, the four resulting cells consequently having one plastid each. In the third cell-division the plastids also divide, so that each cell of the 16-32-celled structure developing from the zygote has its single plastid. Each of the cells eventually becomes a zoöspore which germinates to produce a new *Coleochæte* body with a single plastid in each cell, the plastid dividing with the nucleus at each cell-division.

A somewhat similar regularity in the behavior of the plastid is shown in *Anthoceros* (Davis, 1899; Scherrer, 1914). Each gametophytic cell contains a single plastid which divides with the nucleus at each cell-division. The egg likewise contains a plastid, but the spermatozoid has none; the zygote and sporophyte cells which it later forms are, therefore, characterized, like the cells of the gametophyte, by the presence of one plastid. Although it is difficult to demonstrate the plastid in the young sporogenous cells, every sporocyte shows one very clearly. As shown by Davis (Fig. 32), the sporocyte plastid divides twice during the prophase of the first division of the sporocyte nucleus, so that each spore of the resulting quartet receives one. Upon germination the spore produces a gametophyte with one plastid in each cell, and the cycle is complete.

In all of the foregoing examples it is evident that the plastids, as stated by Scherrer for *Anthoceros*, remain as morphological individuals throughout the whole life cycle, multiplying exclusively by division. A similar claim is made for the plastids of mosses by Sapěhin (1915), who has also studied the behavior of the plastids in *Selaginella* and *Isoëtes* (1911, 1913). In such cases the plastids possess an individuality comparable to that of nuclei, from which they differ conspicuously, however, in undergoing no fusion at the time of syngamy. The constancy in number is nevertheless maintained by the degeneration of the plastids of one gamete in *Zygnema*, by their failure to divide at one cell-division in *Coleochæte*, and because of the fact that the male gamete carries no plastid in *Anthoceros*. It appears to be generally true that, while the eggs in all plant groups contain plastids (usually leucoplasts), the latter are present in male gametes in certain algæ only. In *Ginkgo* (Mann, 1924) each microspore regularly receives about one-fourth of the plastids of the sporocyte, but the behavior of these bodies throughout the rest of the life cycle has not been ascertained.

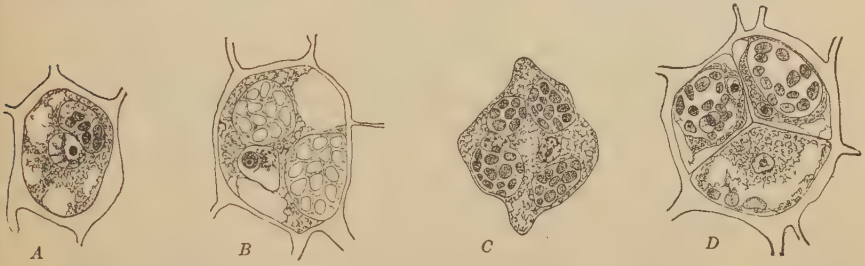

Fig. 32.—The behavior of the plastid during sporogenesis in *Anthoceros*. *A*, sporocyte with single nucleus and plastid. *B*, plastid divided; nucleus in prophase of mitosis. *C*, plastids divided to four; first nuclear division completed. *D*, three of the four spores, each with a single plastid and nucleus. (*After B. M. Davis*, 1899.)

It should be said that only in a comparatively few specialized forms has a genetic continuity of the plastid throughout the life cycle actually been demonstrated. A number of investigators, working on a great variety of plants, have been forced to conclude that plastids are either formed *de novo* as well as by division, or are carried through certain stages of the cycle in some less conspicuous form. Thus in recent years there have appeared many descriptions of the development of plastids from minute primordia in the cytoplasm.[1] As an example may be cited the work of Randolph (1922), whose term *proplastid* will be used for the plastid primordium.

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[1] Lewitsky, Guilliermond, Dangeard, Emberger, Noack, Friedrichs, Mottier, Randolph, and others.

Randolph made a study of the meristematic tissue of young stems and embryonic leaves of *Zea Mays*, which he was able to maintain in the living condition under the highest powers of the microscope for a considerable length of time. All meristematic cells contain proplastids, which appear as sharply distinct refractive globules of varying size, and which may be carried about by the actively streaming cytoplasm. As the cells differentiate the proplastids gradually enlarge, develop chlorophyll, and become the chloroplasts, many stages being observable in a single cell (Fig. 33). Starch appears within them while they are still very small (Fig. 39). Several investigators have expressed the opinion that plastid primordia are permanent organs multiplying only by division, but in *Zea* Randolph found that they grade off to the lower limit of microscopic visibility. Consequently, it is not only difficult to obtain satisfactory evidence for the division of the smallest visible proplastids, but it is wholly impossible to determine by direct cytological observation what may be their history before they have passed above the limit of visibility. As Randolph says:

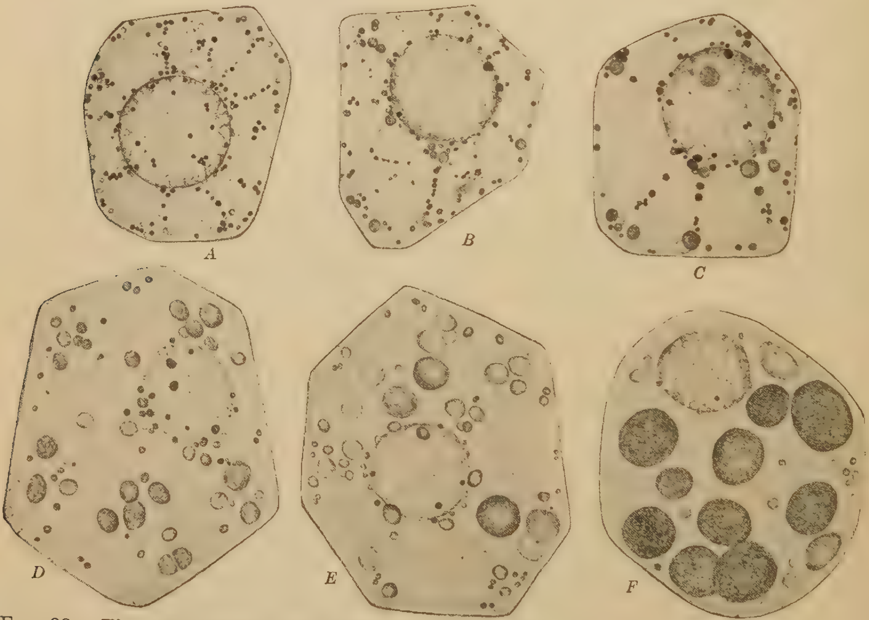

FIG. 33.—The development of chloroplasts from their primordia (proplastids) in the mesophyll of *Zea Mays*. (*After Randolph*, 1922.)

> . . . partially developed and fully matured plastids may be seen multiplying by division, but when first visible the proplastid is so minute that it is impossible to determine the mode of its origin. The division of partially mature and mature plastids emphasizes the fact that they have a distinct individuality at

such stages; but in view of the obscurity which surrounds the origin of the minute primordia from which the plastids first appearing in the embryonic cells arise, the question regarding the extent to which the plastids are to be considered permanent cell organs with an unbroken genetic continuity throughout the life cycle must remain an open one.

Such is the status of the problem of the origin and individuality of plastids in vascular plants. It may be remarked that cytologists have often been inclined to underestimate the capacity of protoplasm for epigenetic differentiation, and so have been too averse to the idea of origin *de novo*. If plastids represent regional transformations of the cytoplasm resulting from the localization of certain processes, they may well be expected to differentiate anew as these processes begin, and to preserve varying degrees of permanence depending upon the processes carried on (Harper). Their individual continuity through certain life cycles would, accordingly, be interpreted to mean that in such forms there is a persistence of certain types of physiological activity through all stages. Such questions are of obvious importance to the geneticist seeking to explain the peculiar inheritance of certain characters manifested in plastids. "If plastids are not passed on as permanent individuals, some other explanation must be offered for their repeated appearance and regular behavior in successive generations" (Randolph).

This whole problem has been greatly complicated by the frequent claim that the plastid primordia are members of a class of cytoplasmic bodies known as chondriosomes, and that therefore "plastids arise from chondriosomes."[1] This matter will be discussed in the latter part of the following chapter. It may be pointed out that the minuteness of these and other elements has led to the confusion of a variety of cell constituents, and that many investigators are in favor of the view that plastids are protoplasmic organs which are fundamentally distinct, probably from their earliest stages, from the many other bodies to which the term "chondriosome" has been applied.[2]

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[1] Lewitsky (1910), Forenbacher (1911), Pensa (1910, etc.), Guilliermond (1911*b*, etc.), Moreau (1914), Nassonow (1918), Emberger (1920), Alvarado (1923), Friedrichs (1922).

[2] Meyer (1911), Dangeard (1919, etc.), Lundegårdh (1910), Mottier (1918, 1921), Scherrer (1914), Noack (1921), Harper (1919), Löwschin (1913, 1914), Sapěhin (1915), and others.

# CHAPTER VI

## CHONDRIOSOMES

Chondriosomes, or mitochondria, are small granules, globules, rods, and threads almost universally present in cytoplasm. They had no single discoverer: the elements described by many early observers correspond with them in some degree. Thus the "fila" of Flemming (1882), the "plastidules" of Maggi (1878) and Zoja (1891), the "bioblasts" of Altmann (1890), and the "cytomicrosomes" of Strasburger (1882) and others are all recognizable among the chondriosomes of today. For a considerable period little attention was devoted to them, largely because of the interest centered in the nucleus and the inadequacy of nuclear methods for the study of cytoplasmic elements. In 1897 and the following years Benda, through the use of newly devised technical methods, discovered chondriosomes in cells of many types, notably in the spermatogenous cells of animals, and applied to them the term "mitochondria." But it was not until a decade later, through the researches of Meves, Regaud, Fauré-Fremiet, Lewitsky, Guilliermond, and others, that they came into prominence. Since that time they have been very intensively studied, and a special literature of large volume has developed. Owing to the difficulties attending the observation of such minute objects and the determination of their relation to other cytoplasmic constituents, opinion regarding the origin, behavior, and biological significance of chondriosomes is still in a very unsettled state.[1]

**Occurrence.**—Although when first discovered chondriosomes were believed to be rather limited in distribution, they have now been reported in plants and animals belonging to nearly all of the larger natural groups.

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[1] Reviews of the subject are given by Fauré-Fremiet (1910*a*), Duesberg (1911, 1919), E. Schmidt (1912), Cavers (1914), E. V. Cowdry (1916*a*, 1918, 1924*a*), Meves (1918*a*), Guilliermond (1919*a*, 1921*i*, 1923), Meyer (1920), and Lundegårdh (1922). Duesberg's paper of 1911 gives the literature complete to that date. Giroud (1925) reviews researches on the physical and chemical nature of chondriosomes. A classified summary of Guilliermond's many researches up to 1921 is given by himself (1921*i*), together with a list of works by others in his laboratory. The most valuable single account is that of E. V. Cowdry (1918). It contains an extensive discussion of the characters and behavior of mitochondria, outlines of the principal microtechnical methods employed in their study, lists of the kinds of cells and organisms in which they have been described, and a tabulation of the many confusing terms applied to them. It has been freely drawn upon in the preparation of this chapter. For the effects of various reagents on chondriosomes, see Kingsbury (1912), E. V. Cowdry (1914, 1918), N. H. Cowdry (1917), and Meyer (1920).

It is asserted by N. H. Cowdry (1917) that "in all forms of animals, from amœba to man, which have been investigated with adequate methods of technique, they occur without exception." Their presence has been reported, furthermore, in practically all tissues. In plants it is probable that they are no less universally present, although it has not yet been possible to demonstrate them with certainty in bacteria, Cyanophyceæ, and certain Chlorophyceæ, such as the Conjugatæ and Confervales (Guilliermond, 1915). They are abundant in myxomycetes (N. H. Cowdry, 1918; Lewitsky, 1924), Charales (Mirande, 1919; Riker, 1921), brown algæ (Mangenot, 1920*abde*), red algæ (Nicolosi-Roncati, 1921), fungi, and all the higher groups.

A critical comparison of the chondriosomes of plants with those of animals has been made by N. H. Cowdry (1917), who concludes, contrary to the opinion of Pensa (1914), that there is every reason to regard them as homologous in the two kingdoms. This is also the conclusion of Mangenot and Emberger (1920). Cowdry finds plant and animal chondriosomes to be practically identical in morphology, reaction to fixatives and dyes, and distribution in resting and dividing cells; any conspicuous differences in arrangement seem to be due to the more pronounced polarity of many animal cells. In both cases they are most abundant in the active stages in the life of the cells.

**Physical and Chemical Nature.**—Chondriosomes occur in the cytoplasm as minute granules, vesicles, straight or curved rods, smooth threads, chains of granules, nets, and other more irregular bodies (Fig. 34). These forms should not be thought of as distinct types, for in living cells they can be seen to change into one another, especially when the

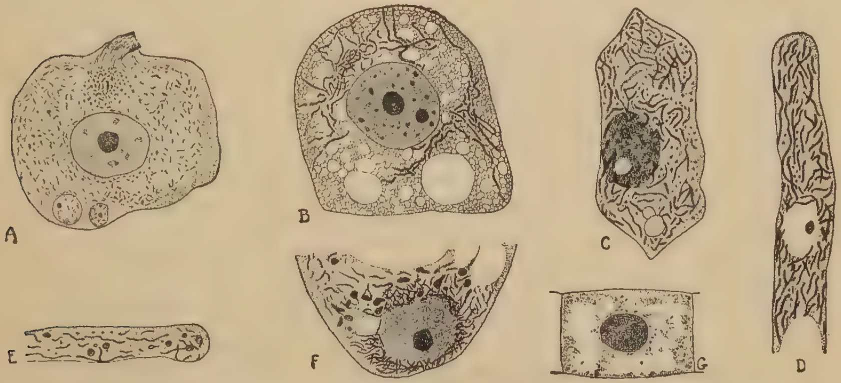

FIG. 34.—Chondriosomes in plant and animal cells. *A*, nerve cell of guinea pig. (*After E. V. Cowdry*, 1914*b*.) *B*, tapetal cell of *Nymphæa alba*. (*After Meves*, 1904.) *C*, living epidermal cell of tulip petal. *D*, ascus of *Pustularia vesiculosa*. *E*, hypha of *Rhizopus nigricans*. *F*, portion of embryo sac of *Lilium;* chondriosomes clustered about nucleus. *G*, cell of root tip of *Allium*. (*C–F after Guilliermond*, 1918.)

cultural conditions are altered.[1] In fixed preparations also they vary somewhat in form according to the fluids employed (Schaxel, 1911; Kingery, 1917). Certain forms do, however, tend to predominate in certain tissues; and although it may be convenient at times to designate rods or threads as "chondrioconts" and chains of granules as "chondriomites," it is to be remembered that the forms assumed by the chondriosomal material are of minor importance. For practically all purposes the now synonymous general terms *chondriosome* and *mitochondrion* are sufficient. The total chondriosomal content of the protoplast has been called the *chondriome.*

The number of chondriosomes present varies greatly with the tissue and the degree of its differentiation. They are usually abundant in young or active cells and relatively few or even absent in fully differentiated ones. In living cells, moreover, they can be seen constantly appearing and disappearing. In her study of the cranial nerves of white mice Thurlow (1917) observed that the number of chondriosomes per unit volume of cytoplasm is constant in corresponding nerves, but not the same in nerves of different types. The arrangement of the chondriosomes within the cell varies, and this is often clearly related to certain functional activities. In certain polarized gland cells, for example, they show an arrangement correlated with the functional polarity of the cells; and if the cells are made to secrete in the opposite direction the position of the chondriosomes is reversed also (Bensley, 1916; E. V. Cowdry, 1918). Such a relation of arrangement to functional polarity apparently does not exist in eggs and nerve cells (Cowdry). Frequently there is a periodic grouping of the chondriosomes about the nucleus, but the significance of this and the means by which changes in position are accomplished are not well understood.

Chondriosomes have a semi-fluid consistency, but actual streaming is not responsible for their change in shape to the extent that some have supposed. If the cytoplasm is not in the gel state they may be centrifuged out, which shows that their specific gravity exceeds that of the cytopltam (Fauré-Fremiet, 1913). In both plants and animals they melt as a temperature of 48 to 50°C. (Policard, 1912; N. H. Cowdry, 1917). In hypotonic solutions they become swollen and vesicular, whereas in hypertonic media they shrink and become slender. Although they may be profoundly altered in appearance by many reagents directly applied, N. H. Cowdry (1920) finds that in growing *Pisum* rootlets subjected to a variety of very abnormal cultural conditions the chondriosomes "are changed to an abnormal degree only under severe conditions which either kill the cell or render its recovery very improbable." In pathological animal tissues they show pronounced qualitative and quantitative changes, of which one of the most characteristic is the breaking up of filaments into granules (see E. V. Cowdry, 1924*ab*).

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[1] Lewis and Lewis (1915, 1924), Chambers (1915, 1924), Anitschkow (1923).

With regard to the chemical nature of chondriosomes, Regaud (1908) Fauré-Fremiet (1910), and Löwschin (1913), working on mammals, Protozoa, and plants respectively, agree that they are a combination of phospholipin and albumin. The same is true in myxomycetes (Lewitsky, 1924). They closely resemble phosphatids, which are combinations of phosphoric and fatty acids, glycerol, and nitrogen bases. Such a compound is lecithin, out of which Löwschin made "artificial chondriosomes" in salt and albumin solutions. Besides staining with hæmatoxylin and several other dyes commonly employed with fixed material, the chondriosomes show a characteristic affinity for certain intra-vitam stains, such as Janus green B, Janus blue, Janus black I, and diethylsafranin, the reaction with the first of these being especially strong. After certain treatments the chondriosomes may closely resemble the "chromidial substance," or granules of nucleo-protein observed in the cytoplasm of some cells. That the two are not to be confused has been emphasized by Duesberg and by E. V. Cowdry. According to the latter author (1916), chondriosomes are "a concrete class of cell granulations," and may be provisionally defined as "substances which occur in the form of granules, rods, and filaments in almost all living cells, which react positively to Janus green and which, by their solubilities and staining reactions, resemble phospholipins and, to a lesser extent, albumins." Although slight diversities in composition occur in different organisms, tissues, and stages of development, this characterization appears to hold universally.

**Origin and Multiplication.**—The question of the origin and multiplication of chondriosomes has been much debated. Evidence for their division in somatic cells has frequently been reported, and some investigators have even held this to be their sole mode of origin—that they arise only from preëxisting chondriosomes and are, therefore, permanent cytoplasmic organs.[1] Others have seriously questioned the evidence for division, and are convinced that, whether or not division occurs, chondriosomes arise *de novo* in the cytoplasm.[2] Scherrer observed that the sporocyte and apical cell of *Anthoceros* contain no chondriosomes, these arising later in cells a little removed from the apex. By a third group of workers it has been maintained that they arise in one way or another from the nucleus, particularly in male sex cells.[3] It seems probable that this view is due to a confusion of chondriosomes with granules of nucleoprotein (chromidia), and to a misinterpretation of their tendency to form temporary accumulations about the nucleus.

[1] Guilliermond (1912*a*), Terni (1914), Moreau (1914), Duesberg (1911), Arnold (1912), Friedrichs (1922).

[2] Lewitsky (1910), Forenbacher (1911), Orman (1913), Löwschin (1913), Scherrer (1914), Beckwith (1914), Chambers (1915), Lewis and Lewis (1915), Twiss (1919), Meyer (1920).

[3] Tischler (1906), Wassilief (1907), Jordan (1911), Alexieff (1917), von Derschau (1915), Kuschakewitsch (1913), Schreiner (1915), Saguchi (1920*b*), Riker (1921).

Recent researches on chondriosomes, particularly those carried out on living material (Chambers, Lewis), leave little doubt that these bodies may appear anew and be consumed in connection with anabolic and catabolic processes occurring in the protoplasm. It is also probable that they may undergo division occasionally, since they are known to fragment as the result of certain experimental conditions. From his observations on myxomycetes (fixed material) Lewitsky (1924) concluded that the chondriosomes, which are capable of division, may become progressively smaller until they pass below the limit of visibility, and that by growth they may pass the limit in the reverse direction, giving the appearance of origin *de novo*. On the whole it seems that the question of ultimate origin depends on the unknown behavior of invisible bodies, and that such division as may be observed is a passive process rather than the act of autonomous organs.

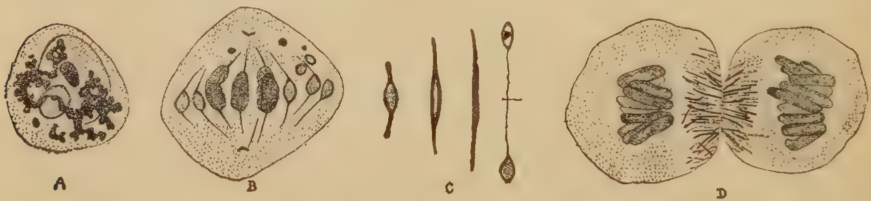

FIG. 35.—Examples of regular behavior of chondriosomes in cell-division. *A–C*, spermatocyte of *Gryllotalpa vulgaris: A*, chondriosomal material in cytoplasm; *B*, first meiotic mitosis, showing chondriosomes (at sides) occupying the achromatic figure with the chromsomes (at center); *C*, stages in the division of a chondriosome. (*After Voïnov*, 1916.) *D*, dividing cell of *Geotriton fuscus*, showing division of chondriosomes as cell constricts at equator. (*After Terni*, 1914.)

It is in dividing cells, particularly animal spermatocytes, that appearances most suggestive of more regular chondriosome division are found. In ordinary tissue cells the distribution of chondriosomes to the daughter cells seems to be more or less fortuitous, though it is usually more or less equal (Nassonow, 1918, on root tip cells). In the spermatocyte of the grasshopper, *Dissosteira carolina* (Chambers, 1915), and the microsporocyte of the larch, *Larix europea* (Devisé, 1922), the chondriosomal material forms a mantle about the nucleus and the mitotic figure, and is separated into two approximately equal portions which then invest the daughter nuclei. In other spermatocytes the chondriosomes are reported to undergo individual division after the division of the chromosomes.[1] In *Euschistus* (Montgomery, 1911; Brown, 1920) the chondriosomal rods and threads are seen to be passively cut into two parts by the constriction furrow, but in *Gryllotalpa borealis* (Payne, 1916) they break and move apart before the furrow appears. In *Gryllotalpa vulgaris* Voïnov (1916, 1925) states that the "mitochondria" fuse to form a "mitochondrial spireme," which then segments into 60 or more "chondriosomes."

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[1] Fauré-Fremiet (1910), Korotneff (1909), Terni (1914), Payne (1916).

These units are arranged on the spindle along with the chromosomes, which they may closely resemble, divide at both meiotic divisions, and are thus equally distributed to the four resulting spermatids (Fig. 35, *A-C*).

In certain scorpions, also, the chondriosomal material of the spermatocyte is distributed with remarkable precision (Wilson, 1916). In *Centrurus* (Fig. 36) it takes the form of a single ring-shaped body which lies by the side of the spindle figure. It divides accurately at both meiotic divisions along with the chromosomes; each of the four spermatids, and hence each spermatozoön, receives a quarter of its substance. In *Opisthacanthus* about 24 hollow spherical bodies are formed instead of a ring. These show no evidence of division, but are separated into four approximately equal groups by the cell-divisions, each spermatid receiving six (occasionally five or seven). A European species described by Sokolow (1913) agrees essentially with this. Mark and Wyman (1922) report that in a grasshopper, *Chorthippus curtipennis*, the spheroidal chondriosomal bodies at each meiotic division form a ring which lies equatorially around the spindle figure and separates into two parallel rings before the cell constricts.

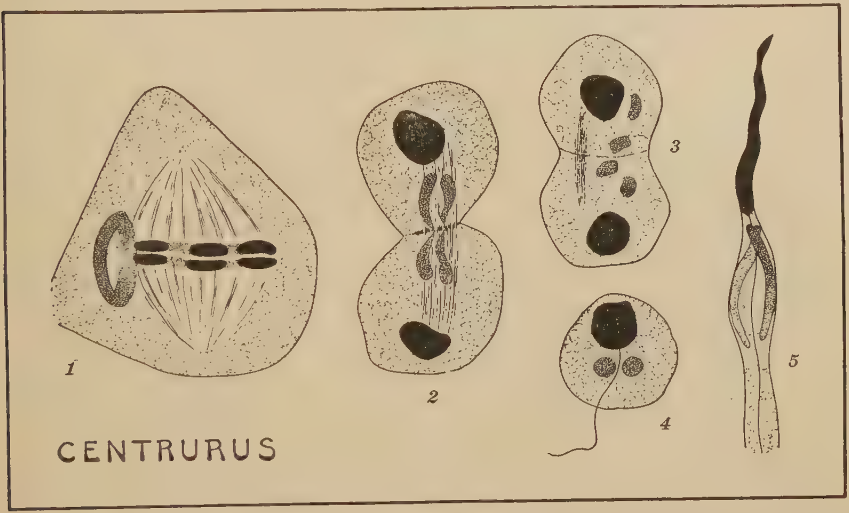

FIG. 36.—The division of the chondriosomal material (chondriokinesis) in the spermatocyte of *Centrurus*. 1, metaphase of first meiotic mitosis; chondriosomes in the form of a ring. 2, close of first mitosis; the chondriosomal ring has divided into 4 parts. 3, second meiotic division, showing 2 of the 4 spermatids, and 4 of the 8 parts into which the ring divides. 4, spermatid with double chondriosomal body, or nebenkern. 5, nebenkern elongating to form tail envelope. (*After E. B. Wilson*, 1916, 1923.)

**The Function of Chondriosomes.**—Our knowledge of chondriosomes is far too incomplete to warrant any categorical assertions concerning their function. The literature is not only complicated by conflicting statements regarding their observed behavior, but it is further encumbered with a variety of hypotheses, many of which rest on very narrow foundations. In this section we shall do little more than pass in review some of the more prominent opinions.

Meves in 1908 propounded a general theory according to which all the visible differentiations which develop in different types of cells during ontogenesis are modifications of the same elementary cytoplasmic constituents, namely, the chondriosomes. Not only are these concerned in the formation of fibrils, plastids, and the like,[1] but they play an important rôle in heredity also. This theory of differentiation was adopted by a considerable number of investigators. Benda (1899), Meves (1907*ab*, 1909), and particularly Duesberg (1909*ab*) observed the close association of chondriosomes with myofibrils, and their claim that the fibrils were actually transformed chondriosomes received rather wide support. Similarly, the chondriosomes have been thought to be closely concerned in the formation of neurofibrils (Meves, 1907*a*; Hoven, 1910*a*; G. Arnold, 1912), collagenic fibrils of connective tissue (Meves, 1910), and epidermal fibrils in chick embryos (Firket, 1911). This interpretation of the genesis of fibrils has been adversely criticized.[2] Thus in the case of myofibrils Gaudissart showed that the chondriosomes in some way coöperate in their development, but do not furnish their primary basis. In tissue cultures the chondriosomes seem to be quite independent of growing fibrils in mesenchyme cells (Levi, 1916), and the same is true of collagenic fibrils in connective tissue (Lewis, 1917). In the case of neurofibrils, furthermore, Cowdry has demonstrated the inadequacy of the evidence for their chondriosomal origin; in fact, it now seems that these fibrils do not exist as such in living nerve cells. One of the clearest examples of the close association of chondriosomes with a special cytoplasmic differentiation is seen in the animal spermatid, where the chondriosomal material aggregates to form a "nebenkern," which, in turn, becomes the principal constituent of the tail sheath of the spermatozoön (see Chapter XIV). According to Krjatchenko (1925) the protruberances covering the pollen grain of *Lilium* are due to chondriosomal action (see p. 220).

Observations on cells of many types have led to the conclusion that chondriosomes are not only concerned in the development of structural differentiations such as those mentioned above, but also play an important rôle in the elaboration of secretion and storage products, forming such substances in somewhat the same manner that plastids form starch. Perhaps most plausible on chemical grounds is the view that chondriosomes give rise rather directly to fatty products, which form an important constituent of yolk spherules.[1] Coghill (1915) saw what were apparently chondriosomes arising from yolk globules in living cells of amphibian embryos. Saguchi (1920) associates chondriosomes with fatty globules in pancreas cells.

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[1] A long list of substances supposed to be formed from chondriosomes is given by E. V. Cowdry (1918, p. 102).

[2] Heidenhain (1911), Levi (1911, 1916), Gurwitsch (1913), Gaudissart (1913), E. V. Cowdry (1914*d*, 1918), and others.

The probable rôle of chondriosomes in the elaboration of zymogen in the pancreas has been frequently pointed out. That chondriosomal material actually transforms into zymogen granules was held by Hoven (1910*b*) and Arnold (1912); but Regaud (1911), who with Meves first emphasized the secretory theory in general, recognized the chemical difficulties in the way of such a transformation, and thought it more probable that the chondriosomes synthesized the products from materials selected from the cytoplasm (the "electosome theory"). The results of the experiments of Scott (1916) and Key (1916) are also not in harmony with the transformation hypothesis. Saguchi (1920) states that the chondriosomes in a certain "secretogenous area" between the nucleus and the free end of the cell disintegrate into "prozymogen granules," which enlarge and become zymogen granules. It is the opinion of Morelle (1923) that the chondrioconts (rod-shaped chondriosomes) of the pancreatic cell are not plastid-like in action, but represent a substance elaborated by the protoplasm and then directly transformed into the secretion droplets (Fig. 37). He shares the view of H. Lutz (1921) that the chondriocents in the pancreas may not be homologous with those in embryonic cells, and accordingly calls them "zymoconts."

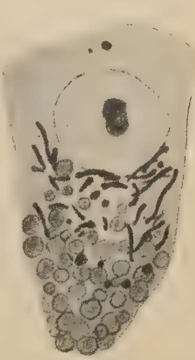

FIG. 37.—Cell of the pancreas of the frog, showing rod-shaped chondriosomes in the middle portion of the cell where the secretion is produced. (*After Morelle*, 1923.)

By those who hold the theory that plastids develop from chondriosomes (Guilliermond and others), such plastid products as starch, pigments, and volatile oils are also regarded as primarily chondriosomal in origin. This point will be considered later in the chapter.

The theory that chondriosomes are in any sense protoplasmic organs with special rôles in differentiation and secretion is strongly opposed by A. Meyer (1911, 1920), who contends that they are simply ergastic accumulations of an albuminous nature.[2] Their ergastic nature, according to Meyer, is indicated by the fact that their distribution and behavior

[1] Loyez (1909), Dubreuil (1913), van Durme (1914), Shaffer (1920), Gatenby and Woodger (1920), Hibbard (1922).

[2] Meyer (1920) calls any microscopically visible ergastic mass an *Ant*. Plant chondriosomes, which he claims are composed of non-crystalline albuminous "allin," are consequently termed *Allinante*. Similarly, he speaks of *Zellsaftante* (droplets of cell sap), *Fettante* (fat globules), *Sekretante* (secretion globules or granules), *Eiweissante* (albumin masses, crystalline or non-crystalline), *Kohlehydratante* (carbohydrate masses), and so on. He regards Allinante as analogous to animal chondriosomes.

are just what would be expected of reserve substances necessary as sources of building material and energy (in meristematic cells, eggs, regenerating tissues, muscles, etc.). They do not transform into "alloplasmatic" differentiations such as myofibrils, but they lie near them and furnish materials or energy for their upbuilding by the cytoplasm. They do not elaborate or secrete the ergastic substances which appear in protoplasm (fat, zymogen, etc.), but they are themselves those substances in the early stages of formation by the cytoplasm. Theories of the histogenetic and secretory functions of chondriosomes are attributed to the similarity in form, position, and staining reactions of reserve masses and developing alloplasmatic structures, and to a confusion of chondriosomes with plastids and other small bodies from which they are fundamentally distinct. The general view that chondriosomes are products of metabolic activity rather than distinct protoplasmic organs has been held in one form or another by many workers, and appears to be well supported by many observations on both living and fixed cells.

The almost universal occurrence of chondriosomes in protoplasm suggests a connection with some fundamental process common to all living matter. That this process may be oxidation, the chondriosomes being a "structural expression of the reducing substances concerned in cellular respiration," was suggested by Kingsbury (1912), who pointed out that they are best fixed by oxidizing agents depending for their effect on reducing substances, probably the lipoidal chondriosomes, in the cytoplasm. The chemical fitness of chondriosomes for processes involving oxidation and reduction was further emphasized by the work of Mayer, Rathery, and Schaeffer (1914), who also pointed out that various reagents which diminish respiratory oxidations attack lipoids. The observations of E. V. Cowdry on the action of vital dyes are also in harmony with this interpretation. Evidence regarded as unfavorable to the respiration theory has been brought forward by Kropp and May (1924). These investigators find that the chondriosomes in the white blood cells of animals made to inhale oxygen, carbon dioxide, and ether differ in no discernible way (Janus green method) from those of normally respiring animals; and they think it probable that alterations observed by others in gassed animals are not direct effects of respiratory conditions. They incline to the theory of Marston (1923) that chondriosomes are centers of enzyme production.

One of the most striking views regarding chondriosomes is that they are microörganisms. Altmann (1890) thought many years ago that protoplasm was essentially a vast colony of living "bioblasts" (in part the chondriosomes) in a non-living ground substance. Very recently Portier (1917, 1918) and Wallin (1922–1925) have independently suggested anew that "mitochondria are, in reality, bacterial organisms, symbiotically combined with the tissues of higher organisms." Wallin finds evidence for this view in the fact that bacteria and chondriosomes show certain similarities in form, staining reaction, chemical composition, physical properties, and function, and in peculiarities in the development of *Bacillus radicicola* in the cells of the clover nodule. Assuming that chondriosomes develop into plastids, Wallin suggests further that chloroplasts are not organs developed in the cytoplasm, but chlorophyll-forming organisms that have invaded protoplasm, with which they live in a state of complete symbiosis.

The bacterial theory has been severely criticized.[1] Cowdry (1923*a*) has clearly demonstrated that chondriosomes and bacteria simultaneously present in the clover nodule show distinct differences in fixing and staining reactions, indicating that a great gap exists between the properties of chondriosomes and those of organisms which have developed the highest degree of symbiosis known to us (Cowdry, 1924*a*). Bowen cites as further evidence against the bacterial interpretation the remarkable behavior of the nebenkern (chondriosomal material) in the animal spermatid. Wallin attributes the peculiar properties of chondriosomes to their long symbiotic history, and is inclined to interpret the nebenkern as a stage in the bacterial cycle somewhat analogous to the "symplasm" in other bacterial forms (Löhnis). He reports further that experiments appear to indicate that chondriosomes can be cultivated independently on nutrient agar. The evaluation of this evidence is awaited with the greatest interest.

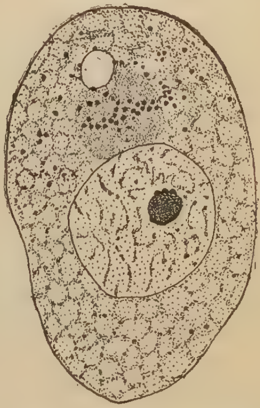

Fig. 38.—Egg of *Filaria papillosa*, showing chondriosomes brought in by the spermatozoön becoming distributed in the cytoplasm. (*After Meves*, 1915.)

A certain group of investigators, notably Meves (1908, 1911, 1914*a*, 1918*b*), have advocated the theory that the chondriosomes play an important rôle in the hereditary transmission of cytoplasmic characters. It had been observed that an enucleated egg might show certain maternal developmental characters after fertilization by a sperm (Godlewski), and it seemed only natural that this should be due to chondriosomes, which Meves regarded as permanent elements multiplying only by division and developing directly into the many structures arising in differentiating cells. The idea received further support when it was found that the spermatozoön almost always carries chondriosomal material into the egg (Fig. 38). The theory in its original form has been weakened by the growing probability that chondriosomes do not have an unbroken genetic continuity, and by uncertainties regarding their relation to differentiation and their value in the spermatozoön; but it is not at all improbable that even as temporary constituents of the protoplasmic system they may be concerned in those fundamental reactions through which all inherited characters, whatever the degree of their dependence upon particular cell organs, are brought to expression. It can scarcely be denied that characters peculiar to the cytoplasm may depend very largely upon substances limited to that portion of the protoplast, whether or not those substances are constantly present in visible form.

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[1] Regaud (1919), Guilliermond (1919*c*), Cowdry and Olitsky (1922), E. V. Cowdry (1923*a*), Bowen (1923), Nicholson (1923), and others.

This leads directly to the problem of the relation of chondriosomes to plastids.

**Chondriosomes and Plastids.**—The general theory of Meves that all intracellular differentiations are due to transformations of fundamental protoplasmic elements, the chondriosomes, was extended to plants by Lewitsky (1910, etc.) Pensa (1910, etc.), and others, who developed the conception that chondriosomes develop directly into plastids. In *Pisum* and *Asparagus*, for example, Lewitsky concluded that chondriosomes become leucoplasts in the root and chloroplasts in the stem and leaf. Further evidence was brought forward by Forenbacher (1911), Moreau (1914, 1915), Cavers (1914), Emberger (1920), Friedrichs (1922), Alvarado (1923), and others. Particularly noteworthy are the extensive researches of Guilliermond (1911–1924), who has contributed largely to the literature on the subject.[1] The chondriosomes, according to the view of Guilliermond, arise only from preëxisting chondriosomes by division, persist in the gametes and through the embryonic stages, and during development perform a variety of functions. Some of them

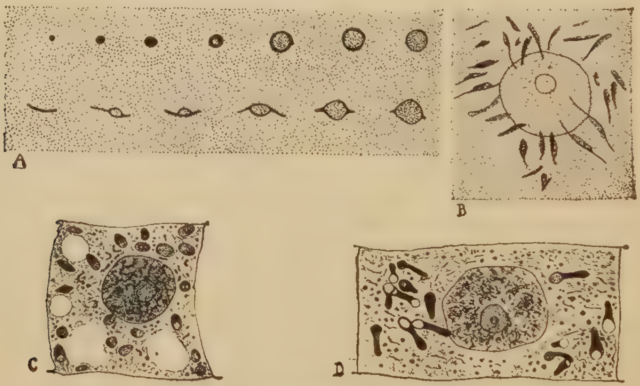

Fig. 39.—*A*, formation of fat by granular and rod-shaped chondriosomes in the rabbit. (*After Dubreuil*, 1913.) *B*, formation of needle-shaped crystals of carotin in chromoplasts supposedly derived from chondriosomes in epidermis of *Iris* petal. (*After Guilliermond*, 1918.) *C*, chondriosomes and chloroplasts in young cell of *Pinus*. *D*, transformation of plastid primordia into leucoplasts, some of them containing starch, in the root of *Pisum*. (*C and D after Mottier*, 1918.)

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[1] See footnote at beginning of chapter.

develop into leucoplasts and chromoplasts of various types, while others remain relatively small, elaborating oils and other products which appear in the cells as they differentiate (Fig. 39). Emberger (1920*c*) and Friedrichs (1922) report that under certain conditions plastids may in turn become chondriosomes.

The development of plastids from minute primordia has already been described (Chapter V), and it has been shown that equally minute bodies represent, or are somehow concerned in the development of other substances in protoplasm. The chief question at issue is that of the relation of these two classes of bodies: are they fundamentally the same, plastid primordia being only chondriosomes which develop in a certain way, or are they fundamentally distinct, merely resembling each other because of their minuteness?[1]

Because of their prominence in the literature, special attention may be given to the views of Guilliermond and the Dangeards, who have investigated a great variety of plant cells. According to Guilliermond, all plant cells contain three principal classes of cytoplasmic bodies: (1) the *chondriome,* comparable to that of animal cells, and comprising chondriosomes of two kinds multiplying only by division; those of one kind (*a*) are active elaborative elements and develop into plastids, while the others (*b*) are relatively inactive and of uncertain function; (2) *lipoid globules,* bearing no relation to the chondriome; and (3) the *vacuolar apparatus,* which often begins its development in the form of minute non-chondriosomal bodies, and which later contains various elaborated products. P. A. and P. Dangeard also distinguish three constant cytoplasmic elements: (1) the *plastidome,* comprising all the plastids of the cell, which begin their development as minute bodies and multiply only by division;[2] (2) the *cytome,* or assemblage of "cytosomes," which appear to give rise to fat and oil or to undergo no visible change;[3] and (3) the *vacuome,* or vacuolar system, which begins its history as small "metachromes" and later contains various products.[4]

The above investigators interpret each other's findings as follows. Guilliermond homologizes his chondriosomes with the mitoplasts of the Dangeards, claiming that these workers have failed to distinguish the active from the inactive ones, and holds their cytosomes to be the same as his lipoid globules. According to the Dangeards, on the other hand, the "active chondriosomes" of Guilliermond (and the chondriosomes of other workers in general) are mitoplasts, his "inactive chondriosomes" are cytosomes, and his lipoid globules are ergastic materials not included in the three classes of constant cytoplasmic elements. There is general agreement on the vacuolar system. Although Guilliermond held for a time that anthocyanin pigments, tannin, and metachromatic corpuscles were produced by chondriosomes, he now agrees with the Dangeards that the elements in which they arise belong to the vacuolar system. This, as P. Dangeard (1923) points out, reduces the supposed elaborative rôle of Guilliermond's chondriome to the production of starch, plastid pigments, and certain oils. This is a further indication of the distinctness of the plastid class of cytoplasmic bodies.

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[1] The first alternative is upheld by Meves, Lewitsky, Guilliermond, and their followers, and the second by Meyer (1911, 1920), P. A. and P. Dangeard (1919, etc.), Lundegårdh (1910), Scherrer (1914), Sapěhin (1915), Noack (1921), Harper (1919), Mottier (1918, 1921), Löwschin (1913, 1914), and others.

[2] These are referred to as "spheroplasts," "discoplasts," or "mitoplasts," according as they are spherical, discoid, or filamentous.

[3] Before 1924 the Dangeards used the terms "spherome" and "microsome" rather than "cytome" and "cytosome." Spherical and elongated cytosomes are called respectively "spherosomes" and "mitosomes." For a more common use of the term "cytosome," see p. 57.

[4] On the basis of form the metachromes are classified as "spherochromes" and "mitochromes."

Other researches bearing on this point are those of Mottier (1918, 1921), Emberger (1920, 1921, 1922, 1923), and Meyer (1920). In several liverworts and seed plants Mottier finds that leucoplasts and chloroplasts are derived from small rod-shaped primordia which are permanent organs multiplying by division, and that there is a second class of permanent elements which probably function in metabolism. Emberger, working with ferns, likewise finds two classes of elements which he claims are visibly distinct; those of one class become plastids and the others do not. · Meyer finds that the plastid primordia are microchemically very similar to the other elements, but distinguishes them on the basis of their peculiar movements and their development of pigments and starch. It is obvious that these and other investigators have observed the same groups of objects, but have differed widely in their use of terms. Guilliermond and Emberger call both classes—the plastid formers and the albuminous elements of uncertain function—chondriosomes, though of different types. Meves calls only bodies of the first class chondriosomes, which he regards as equivalent to those of animals; those of the second class he holds to be lifeless inclusions. Meyer calls the first class plastids, and the second Allinante, a special class of ergastic inclusions equivalent to the chondriosomes of animals. Mottier originally spoke of the first class as plastid primordia and the second as chondriosomes, but in view of the loose use of the latter term he drops it in his paper of 1921. The Dangeards call the first class mitoplasts and the second cytosomes, disapproving of the terms chondriosome and mitochondrion because of their indiscriminate application to small bodies of many types.

In view of the obscurity surrounding many points, any conclusions on this subject must be more or less arbitrary. But it is of service to have in mind some tentative scheme of classification for cytoplasmic differentiations and inclusions. Considering present probabilities, such a scheme may be somewhat as follows: (1) *plastids*—true protoplasmic organs distinct from all other bodies, arising from minute primordia (proplastids) of uncertain origin and multiplying by division; (2) *chondriosomes*—a special class of elements composed of phospholipin and albumin, closely resembling proplastids in appearance and composition; (3) *vacuolar material*—an accumulation of water with various ergastic substances in solution, often arising from minute bodies of uncertain history; (4) *other ergastic bodies*—many chemically diverse products of metabolic activity. This scheme, which, it will be observed, embodies the conceptions of Meyer and the Dangeards, is drawn up with particular reference to plants, but with certain qualifications regarding plastids and the vacuolar system (see next chapter) it applies to animals as well. It remains for further research to show to what extent Meyer's contention that chondriosomes, along with vacuoles and all other visible inclusions except plastids, are ergastic in nature, and to evaluate the claim of the Dangeards that vacuoles are autonomous elements. The principal question at issue, namely, the exact relation of plastids to chondriosomes at the time of their first appearance in the cytoplasm, is also an open one, but we have made the temporary disposition of it which at present seems safest.

**Conclusion.**—In conclusion it may be said that the state of our knowledge of chondriosomes shows a small but encouraging improvement, in that we are becoming somewhat more clearly aware of certain distinctions betwen plastids, vacuolar elements, chondriosomes, and other ergastic bodies of various kinds, all of which have been confused with one another in their initial stages and termed chondriosomes by one worker or another. Rather than use this term in an all-inclusive sense or drop it altogether we have chosen to restrict its application to the class of bodies about which most of the obscurity centers. That chondriosomes maintain an unbroken genetic continuity and are to be identified with plastid primorida now seems improbable, though these questions involve the unknown behavior of ultra-microscopic masses of matter. The most plausible hypotheses suggested by their almost universal occurrence in protoplasm are that they bear some relation to respiration, and that they are peculiarly important elaborated products which are employed as sources of matter and energy in further growth and differentiation.

In spite of the fact that the study of chondriosomes has so far raised more problems than it has solved, it has already proved of much value, for it has turned to the cytoplasm some of the attention so long directed almost exclusively to the nucleus; and it appears that many problems of much importance in cytology pertain to the cytoplasm. It has also been of great service in bringing about a closer scrutiny of the effects of fixation and a renewed emphasis upon the importance of the study of living protoplasm. Much has already been learned as the result of this study, but the solution of the principal problems involving chondriosomes must await the results of further research.

# CHAPTER VII

## THE GOLGI MATERIAL

For many years the Golgi material has been chiefly the concern of students of animal tissues, but the interest of botanists has recently been stimulated by evidence of an analogy between this cytoplasmic constituent and the vacuolar element of plants. As in the case of the chondriosomes, one has to deal here with a large number of observations but very few plausible interpretations.[1]

**General Nature and Occurrence.**—The Golgi material takes its name from its discoverer. In 1898 Golgi, using a modification of a method devised by Cajal for the study of nervous tissue, found in the Purkinje cells of the barn owl's brain a structure which he called the "internal reticular apparatus." It consisted of a closed net of fine fibrils in a rather definite region of the cytoplasm, intermediate between the nucleus and the cell surface. The net showed occasional nodal enlargements, and fibrils extending toward the nucleus, often with swellings at their ends. Subsequent investigation of a great variety of tissues from many animals

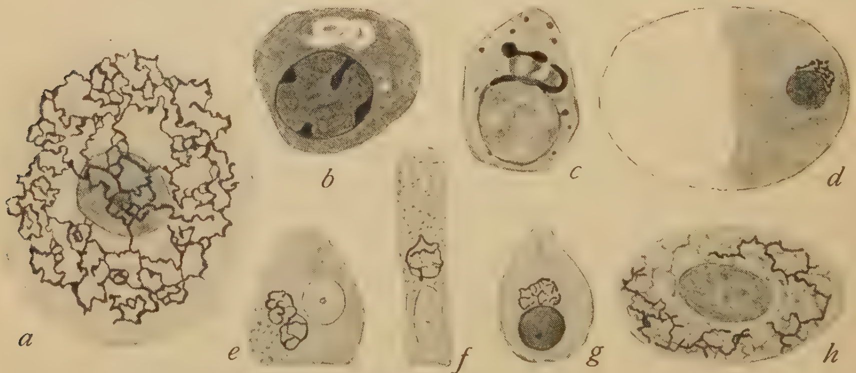

Fig. 40.—The Golgi material in animal cells of various types. *a*, spinal ganglion cell of rabbit. (*After Golgi*, 1899.) *b*, erythroblast of guinea pig, fixed in formalin and potassium bichromate. *c*, the same, fixed in osmic acid. (*b and c after E. V. Cowdry*, 1921.) *d*, fat cell from human skin. (*After Deineka*, 1912.) *e*, cell from pancreas of cat. *f*, epithelial cell from prostate gland of dog. *g*, cartilage cell from cat. (*e–g after von Bergen*, 1904.) *h*, red blood corpuscle of frog, prepared by Golgi's silver impregnation method. (*After Sinigaglia*, 1910.)

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[1] For general accounts, see von Bergen (1904), Duesberg (1914*ab*), Cajal (1914), Pappenheimer (1916), and E. V. Cowdry (1923*b*, 1924*a*). Complete literature lists are given by Duesberg (1914*a*) and Cowdry (1924*a*). For microtechnical methods, see Lee (1921) and Pappenheimer (1916).

showed the "Golgi apparatus" to be of general occurrence, although varying considerably in form (Fig. 40). Commonly it appears as a network or group of fibrils lying at one side of the nucleus or entirely surrounding it. Often it consists only of a few scattered "Golgi bodies," as, for example, in insect spermatocytes. Although the largest and most complex forms are found in vertebrates (spinal ganglion cells), while the simpler non-reticulate forms prevail in invertebrates, there is no constant correlation of form with taxonomic grouping. Furthermore, within some groups the form in different types of tissue is comparatively uniform, whereas in other groups it shows great diversity (Nussbaum). The appearances presented are nevertheless rather characteristic in different cell types and in different stages of development: the "apparatus" is large in gland cells and small in muscle cells; it is well developed in active stages of differentiation, becomes less conspicuous as the cell ages, and may often finally disappear altogether (Cowdry). In pathological or physiologically abnormal tissues it often shows marked alterations, the significance of which is not understood.[1]

The Golgi material seems to be of a watery or semi-solid consistency. Since the centrifuge does not easily displace it, its specific gravity must be about the same as that of cytoplasm (Cowdry, 1922). It is rather remarkable that students of animal tissue cultures and microdissection have never observed it in living cells (Lewis and Lewis, Chambers), and that no known intra-vitam method reveals it (Cowdry). This may probably be accounted for largely on the basis of its close similarity to the cytoplasm in consistency and refractive index. It is soluble in alcohol and blackens with osmic acid, which, together with other reactions, suggests that it consists largely of some lipoid compound (Weigl, 1910, 1912; Nussbaum, 1913; Gatenby, 1920). It is not unlikely, however, that its composition varies considerably in different animals and tissues. It has been chiefly studied after impregnation with silver (Cajal, Golgi) or prolonged immersion in osmic acid (Kopsch), which has given rise to false impressions regarding the nature of the material in the untreated state. After these methods it appears as a brownish or black opaque substance not suggestive of fluidity (Fig. 40, *c*), whereas after other methods (formalin and potassium bichromate) it appears in the form of clear canals (Fig. 40, *b*). The question of the identity of these clear canals and the blackened networks has been much debated. Some have held the two to be distinct (Ross, 1915; Penfield, 1921), at least in some cases (Duesberg, 1920), but others,[2] although they recognize the uncertainty of the situation, are inclined to regard them as identical, and attribute the unexplained differences to technique. Cowdry has bleached out the blackened networks in pancreas cells and found corresponding systems of clear canals remaining; such appearances suggest positive and negative impressions of the same structure. But it is not yet known to what extent this interpretation can be generalized.

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[1] Cowdry (1924*a*) lists the alterations reported by many observers.

[2] Heidenhain (1911), Saguchi (1920), Cowdry (1921*a*, 1923*b*, 1924*a*).

In the spermatogenous cells of insects Bowen (1920) finds that the Golgi material comprises two substances showing decided differences in staining reaction, and Hyman (1923) reports the same condition in *Fasciolaria*. Cowdry (1923*b*) states that there is as yet no evidence that the Golgi material of the somatic tissues of higher vertebrates has this duplex constitution.

It is not strange that the Golgi material and other cytoplasmic elements such as chondriosomes and chromidia should have been confused in the absence of specific methods. Several authors have claimed, for example, that the Golgi and chondriosomal materials are the same, but it now seems very clear that the two are distinct.[1] Similar claims involving chromidia are also untenable. Cowdry (1912, 1916*b*) has succeeded in demonstrating the distinctness of chondriosomes, Golgi material, and Nissl substance (chromidia) in the same nerve cell, and Bowen (1920, 1922) has shown beyond a doubt that chondriosomes and Golgi bodies are independent in spermatocytes.

**Animal Tissues.**—After the early discoveries of Golgi, Cajal, E. Holmgren and Kopsch, numerous investigators, many of them the pupils of these pioneers, undertook the study of a great variety of tissues, and devised several new methods. The Golgi material was found to be well displayed in nervous tissue[2] almost universally, showing particularly complex patterns in the vertebrates. In certain ganglion cells there is a nutritive mechanism consisting of branching and anastomosing cytoplasmic prolongations sent in from the surrounding cells. E. Holmgren (1899) expressed the view that these structures become axially vacuolized to form a system of canals ("trophospongium") communicating with the exterior, and that this is the Golgi apparatus of other authors. This interpretation was at first accepted by several workers, but was later generally opposed, since the Golgi system of other cells was found to arise not by ingrowth from the exterior, or in processes which had so grown in, but rather by a fusion of droplets and filaments in the cell's own cytoplasm (von Bergen, 1904). Moreover, Golgi canals develop in "free" cells, such as white blood corpuscles, which have no surrounding nutritive cells. Holmgren further held that the intracellular canals of muscle cells developed as ingrowths from the exterior, but it now appears that they develop wholly within the cytoplasm of the muscle cell and do not communicate with the exterior. The general conclusion is that the

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[1] Cajal, Saguchi, Nussbaum, Benda, Gatenby, Duesberg, Bowen, Nassonow, Cowdry, Drew, Pappenheimer, Kolmer, and others.

[2] Veratti (1899), von Bergen (1904), Sjövall (1906), Marcora (1908, 1909, 1910), Legendre (1910), Besta (1910), Nussbaum (1913) and his students.

Golgi canals are distinct from any nutritive structures, and that Holmgren confused the two (Nussbaum, Ross, Golgi, Perroncito).

Networks of Golgi material have often been described in connective tissue. In cartilage cells Cajal observed certain alterations in the appearance of the net in cells near the line of ossification. Networks also appear in the megacaryocytes of bone marrow (Maccabruni, 1909), tooth tissue (Massenti, 1914; Cajal, 1914), Descemet's membrane in the eye (Zawarzin, 1909; Deineka, 1912), lymphocytes (Verson, 1908), red blood corpuscles (Sinigaglia, 1910; von Berenberg-Gossler, 1912; Fananas, 1912), and a variety of other cells. In the guinea pig Cowdry (1921) finds that erythroblasts, leucocytes, and lymphocytes all have "a restricted area of fluidity" in the cytoplasm, and that this watery mass seems constantly to undergo changes of shape. In a protozoan, King and Gatenby (1923) find Golgi material in the form of rods which behave like those of the Metazoa at the time of cell-division.

Because of the afforded clues concerning the possible function of the Golgi material, certain phenomena observed in glandular epithelia[1] are of special interest. Ordinarily, the Golgi material lies as a network between the nucleus and the side of the cell from which the secretion is delivered—such glandular cells have a definite physiological and morphological polarity. Cowdry (1922) has made the highly suggestive observation that:

> . . . in the thyroid glands of normal guinea pigs the reticular material is not invariably found between the nuclei and the follicular lumen . . . but in some cases undergoes an active migration to the opposite pole of the cell, which, together with other evidence at hand, indicates the existence of a reversal in physiological polarity whereby the secretion is discharged directly into the circulation, instead of being first stored within the follicles.

Confirmatory evidence is found by Reiss (1922) in the cat's hypophysis, in which alterations in secretory polarity also appear to take place. Several years ago certain changes in the aspect of the Golgi material accompanying secretory phases were observed in cells of the alimentary tract (Kolster, 1913; Cajal, 1914) and the mucus glands of the larynx (Pappenheimer, 1916). The inference that the Golgi material is intimately concerned in the elaboration of secretions is strongly supported, 3
in fact, demonstrated, by the observations of Nassonow (1923, 1924*a*) and Bowen, (1923, 1924*a*) on the pancreas and intestinal goblet cells of amphibans (Fig. 41). The secretion first appears in the form of minute granules or droplets along the strands of the basket-like Golgi network. The droplets pass toward the distal region of the cell, where they collect

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[1] Negri (1899, 1900), Cajal (1903, 1914), Stropeni (1908), Barinetti (1912), Kolmer (1916), Kolster (1913), Pappenheimer (1916), Saguchi (1920*b*), Cowdry (1922), Nassonow (1923, 1924*a*), Bowen (1923).

in large masses and complete their growth. As they move away from the net each is seen to carry with it a small cap or girdle of Golgi material. Whether the Golgi material actually transforms into the secretion products or in some way influences their synthesis from materials derived from other sources (chondriosomes?) is uncertain. In his later researches on gland cells of several other types Bowen (1925) finds that the topography of the Golgi system is rather definitely related to the type of secretion being produced, and that it frequently differs characteristically in cells of the same type in vertebrates and invertebrates. Voïnov (1925) derives the fat globules in the *Gryllotalpa* oöcyte from it. In spite of all of these facts, as Cowdry (1923*b*) remarks, it is not to be concluded that the Golgi material is solely a secretory system, since it is also well developed in cells with no pronounced secretory activity. Of special interest in this connection is the view of Nassonow (1924*b*) that the excretory apparatus (contractile vacuole) of Protozoa is the homologue of the Golgi system of Metazoa.

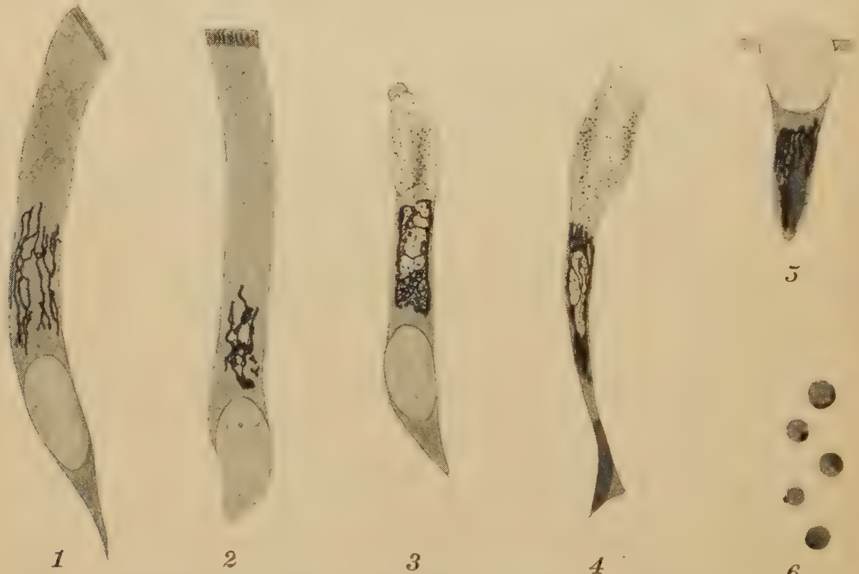

Fig. 41.—The relation of the Golgi apparatus to secretion. 1–5, stages in the formation and accumulation of secretory droplets to form a typical "goblet cell" in the intestinal epithelium of *Molge pyrrhogastra*. 6, individual secretory granules with attached bits of Golgi material in the pancreas of *Cryptobranchus*. (*After Bowen*, 1924*a*.)

The studies of Bowen (1920, 1922*b*) and others have shown that the Golgi material occurs in two general arrangements in spermatocytes. In insects there are a number of separate Golgi bodies scattered throughout the cytoplasm, and each of them is made up of a deeply and a lightly staining portion. In amphibians and certain other animals they are aggregated closely about the centrioles, their lightly staining substance uniting to form a solid mass known as the *idiosome*, on the surface of which the deeply staining portions of the constituent bodies may be distinguished. In the spermatid the Golgi bodies undergo a remarkable transformation, uniting to form an *acroblast;* from this is differentiated and budded off an *acrosome*, which, in turn, becomes in part the *perforatorium* of the spermatozoön. These changes will be described in detail in Chapter XIV. Bowen (1923, 1924*a*) compares the development of the acrosome with the formation of secretion globules in goblet cells, and inclines to the view that it, too, is a secretion of the Golgi material, with a special rôle in fertilization. The behavior of the Golgi material in oöcytes is relatively little known, but some authors have thought it to be concerned in yolk-formation (Hirschler, 1913; Cattaneo, 1914).

**Plant Tissues.**—In 1910 Bensley treated root tips of *Allium, Iris*, and *Lilium* and the tapetum of *Lilium* with fixing reagents (composed chiefly of neutral formalin and potassium bichromate) which he had employed in the investigation of animal tissues, and found a condition very different from that previously described by botanists. In material fixed with ordinary reagents (Flemming, Zenker, Carnoy, etc.) the vacuole seemed to arise by the union of innumerable small droplets, but after fixation in Bensley's fluids it appeared as a unit from the first. In very young cells it had the form of a system of fine canals, often showing a tendency to lie at one side of the cell, with branches ending freely near the periphery. In older cells these "canaliculi" enlarged and gradually coalesced to form the large vacuole (Fig. 42, *A*, *B*). Bensley succeeded in observing the various stages in living cells. In view of the striking resemblance between the vacuolar system and the Golgi canals of animal cells he ventured the suggestion that the two are morphologically and physiologically equivalent.

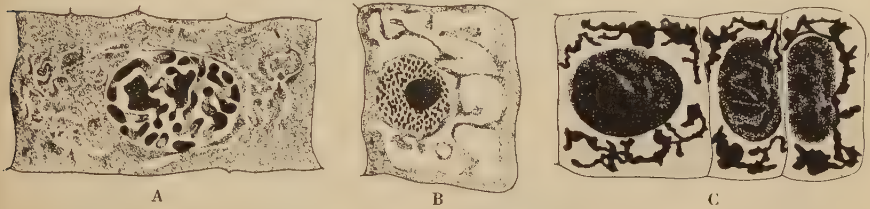

FIG. 42.—*A*, *B*, cells from the root tip of *Allium*, showing development of cytoplasmic canals into vacuoles. (*After Bensley*, 1910.) *C*, cells of the root of barley preserved by the method of Golgi. (*After Guilliermond and Mangenot*, 1922.)

Since the work of Bensley comparatively few investigators have turned their attention to plant tissues.[1] Guilliermond and Mangenot have treated barley roots with the silver impregnation methods and obtained blackened networks corresponding in form with the canaliculi observed by Bensley (Fig. 42, *C*). They, too, regard these stages in the evolution of the vacuolar system as homologous with the Golgi networks of animal cells. Sanchez reports a fragmentation and reconstitution of a rather complicated reticular system in certain phases of cell activity in the epidermis of *Faba vulgaris* seedlings, and is inclined to associate this with the activity of ferments.

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[1] Pensa (1910, 1917), Laburu (1916), Drew (1920), Sanchez (1922), Guilliermond and Mangenot (1922).

The notable researches of P. A. and P. Dangeard (1916-1923) on the development of the vacuolar system in plant tissues treated with vital dyes (see Chapter II) have shown that this system is characterized by a greater definiteness of behavior than had previously been recognized, and as observations on similar tissues treated according to the methods employed by zoölogists accumulate it becomes increasingly difficult to avoid the conclusion that plant vacuolar substance and the Golgi material of animals are more than analogous. The determination of the nature and degree of the relationship is one of the interesting problems with which the future must deal.

**Behavior of the Golgi Material in Cell-division.**—The Golgi material resembles the chondriosomes in being apportioned with various degrees of regularity between the daughter cells at the time of cell-division. The distribution of fragments of the network in dividing spermatocytes was seen by Platner (1889) many years before the nature of the material was recognized, but our more definite knowledge of the process began with the researches of Perroncito (1909, 1910) and Deineka (1912). In the spermatocytes of a snail, *Paludina vivipara*, Perroncito observed the fragmentation of the Golgi network into a number of elongated pieces, which formed a crown-like group and then passed to the daughter cells. He called the pieces *dictyosomes* and the entire process *dictyokinesis*. He reported a similar situation in certain mammals. In opossum spermatocytes, according to Duesberg (1920), the process is much less regular: the network becomes a coiled thread, irregular fragments lie scattered between the two nuclei at anaphase, and the network is reconstructed in the daughter cells. In the insects, on the other hand, Bowen (1920)

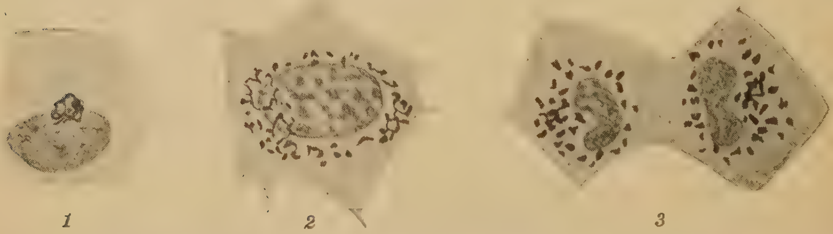

Fig. 43.—The division of the Golgi material (dictyokinesis) in epithelial cells of the Descemet's membrane of the cat. (*After Deineka*, 1912.)

finds that the distribution of the Golgi material is accomplished with much precision. In *Euschistus*, for example (Fig. 143), it does not form a compact idiosome as in many other animals, but consists of scattered plate-like bodies. As the nucleus prepares to divide, these bodies form a circular series at the equator of the cell and fragment individually, after which they pass toward the poles in advance of the chromosomes. In some species they become arranged in two circular series, the migrating chromosomes passing through the rings. Eventually they lie scattered in the daughter cells, and undergo further fragmentation.

The first clear account of dictyokinesis in somatic tissues was given by Deineka (1912). In the connective and epithelial tissues of the cornea in young dogs and cats he observed the fragmentation of the Golgi net into small pieces which were distributed as two groups to the daughter cells (Fig. 43). The process has subsequently been observed in other tissues.

The distribution of Golgi and chondriosomal materials at the time of cell-division appears in many cases to be as fortuitous as that of other substances of an ergastic nature, there being little to suggest autonomous action on their part. The more regular behavior seen in other instances, notably in spermatocytes, is in all probability associated with a greater constancy of the functions involving such materials in these cells. The corresponding phenomena have not yet been studied in plants.

**Conclusion.**—The Golgi material, which appears to be present almost universally in animal tissues and probably varies somewhat in physico-chemical composition, differs from other cytoplasmic components in its tendency to accumulate in the form of canals and networks. The characteristic and relatively fixed pattern of the accumulation in many cells naturally suggested to Golgi that it was a specific cell organ, but this interpretation has not been generally followed. It appears to be the material itself, rather than the canals containing it or the morphological patterns assumed, that is of significance, so that the expressions "Golgi apparatus" and "reticular apparatus" are less appropriate than "Golgi material." It is becoming increasingly probable that the similarity between this material and the vacuolar material of plants indicates true homology rather than mere analogy. In mode of development, form, and reaction to reagents the two are strikingly alike; and the close association of the one with secretory processes strongly suggests the elaboration of pigments and other vacuolar products in the other. The plant differs chiefly in the amount of the material present, and in certain features (osmotic phenomena, storage) which follow as consequences. Should this suggested homology be upheld by future investigations, two fields in cytology would become one, to the certain benefit of all who are working in them.

## CHAPTER VIII

## ERGASTIC SUBSTANCES

In Chapter II emphasis was laid on the conception of protoplasm as a living system of components which of themselves are non-living. It was pointed out that various substances present in protoplasm and having an undoubted effect upon its action can be removed without terminating life; that the same substance may be chemically active at one moment and relatively inactive at another; and that it is scarcely possible to be certain that any inclusion of protoplasm is wholly devoid of influence on the life processes. It is therefore impossible to make any sharp distinction between "living" and "non-living" components. As Sachs long ago insisted, the components are active and passive rather than living and lifeless. It is the entire system of all active substances, and not this or that component, which lives.

It is nevertheless convenient to deal separately with materials which, for the time at least, are relatively inactive. These for the most part are accumulations of the products of protoplasmic activity, and represent by-products, supporting structures, and reserves which are later to be used in metabolism. They are thought of as non-living substances, but to whatever slight degree they affect the action of protoplasm they must logically be regarded as a part of the living system. The same interpretation, it should be added, may be placed upon certain factors in the environment, from which the organism cannot be sharply set apart.

The relatively inactive or "lifeless" substances in or on protoplasm were called *metaplasm* by Hanstein (1868). This term has been commonly employed in this sense, but it has unfortunately been widely used in another meaning (see p. 47). We have, therefore, adopted Meyer's (1896) expression, *ergastic* materials, though we cannot follow him in applying it to everything but certain hypothetical units (see p. 49). One should determine what is ergastic not by chemical composition, but rather on the basis of relative inactivity. It is useful, however, to list the ergastic substances encountered by the cytologist partly under chemical headings.[1]

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[1] For an extensive account of the ergastic materials in plants, see A. Meyer (1920). For the chemistry of plant products, see R. W. Thatcher (1921), Onslow (1923), Czapek (1913, 1920), Molisch (1913), Rigg (1924), and Trier (1924). Ergastic materials are not to be confused with the *ergastoplasm* of Garnier (1897), Prenant (1898–1899), and others. This term was applied to a supposedly very active or "superior" type of protoplasm, nearly the same as the *kinoplasm* of Strasburger (1892). A great variety of appearances, including artifacts, have been described as ergastoplasm. For the literature, see Fauré-Fremiet (1910).

**Carbohydrates.**—The most conspicuous visible carbohydrate materials in plants are starch and cellulose. In many green plants the carbohydrate which is first elaborated by the process of photosynthesis (see p. 101) is not formed more rapidly than it is utilized or transferred to other parts of the body. In such cases, as well as in those species which normally do not form starch, no visible product appears in the chloroplasts. Very commonly, however, more of the carbohydrate is elaborated than is immediately removed, in which event it may be deposited in the form of granules of "assimilation starch" in the chloroplasts. Such starch, which is thus the first visible product of photosynthesis, is transformed by enzymes into some soluble form, usually a sugar, and carried to other parts of the plant, where it is either used at once or retransformed, usually through the agency of amyloplasts, and deposited in the form of "reserve" or "storage" starch. This starch, upon which we depend so largely for food, has a composition expressed by the general formula $(C_6H_{10}O_5)_n$. It exists in the form of granules ranging in size up to about $200\mu$, and varying considerably in appearance, in different plants (Fig. 44). The reserve starch granule is formed within the body of the amyloplast, and is made up of a series of concentric layers successively deposited about a center, or "hilum." In case the granule starts to form near the middle of the amyloplast it may develop symmetrically, but commonly it lies near the periphery and becomes very eccentric in form, owing to the unequal deposition of new material on its various sides. The amyloplast becomes greatly distended as the granule grows, often reaching invisible thinness; in extreme cases it becomes ruptured and remains in contact with the granule only at one side, where all new material is thenceforth deposited. Several granules may start to develop simultaneously in a single amyloplast, later growing together to form a "compound granule"

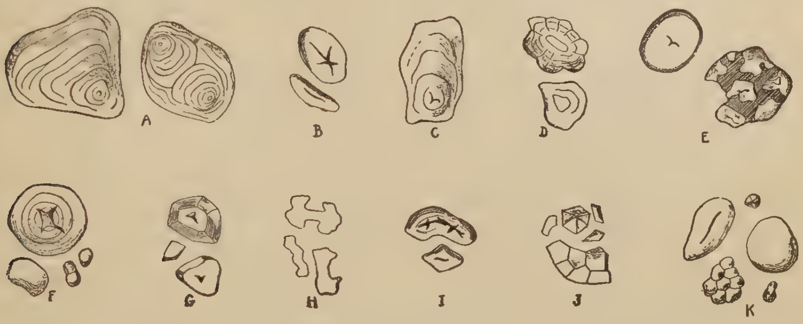

Fig. 44.—Reserve starch granules from various plants. *A*, potato; simple and half-compound granules. *B*, colombo starch. *C*, arrowroot. *D*, pea. *E*, maize; intact and partly digested granules. *F*, rye. *G*, maize. *H*, *Euphorbia*. *I*, bean. *J*, rice. *K*, wheat. (*After Tschirch.*)

with more than one hilum. In case the parts making up the compound granule are enveloped in one or more common outer layers the granule is said to be "half-compound." Potato starch is made up of simple, compound, and half-compound granules, whereas in oats and rice all or nearly all of them are said to be of the compound type. The successively deposited layers making up the granule differ mainly in water content, the innermost layers being richest and the outermost poorest in water. As a result of this non-uniform composition the granule often splits radially when dried.

As a result of his classic researches Nägeli (1858, 1881) developed the theory that the starch granule is made up of ultra-microscopic particles ("micellæ") differing in size and in the thickness of their surrounding water films in the various layers of the granule. He finally decided that the micellæ are crystalline in nature, a conclusion supported by the work of Schimper (1881) with polarized light. This conception of the starch granule as a spherocrystal of radially arranged elements was adopted and elaborated by A. Meyer (1883, 1895), who held the stratification of the granule to be due to differences in the length, thickness, closeness, and richness of branching of the constituent needle-shaped crystals ("trichites"). Both Meyer and Salter (1898) showed that in certain cases the stratification is correlated with the alternation of day and night, and therefore with a periodic activity of the protoplast. The spherocrystal theory has been brought into question by Sponsler (1922), who has employed the newer methods of X-ray analysis. His results appear to show that there is a regular and fairly uniform arrangement of atoms in the starch granule, and that this arrangement is destroyed by crushing, which suggests that the regularity is not that of crystalline structure. In the opinion of Sponsler, either the structure is not sufficiently regular to give definite crystallographic axes (Kabsch, 1863*a*), or the regularity takes the form of curved layers, instead of the planes found in crystals.

Starches vary considerably in composition and reaction to reagents. In ordinary starch the principal constituent is $\beta$-amylose, which turns blue with iodine. With it is a certain amount of $\alpha$-amylose and a little amylodextrin, both of which turn brownish-red with the same reagent. "Red starch" contains more of the amylodextrin constituent, and also amyloerythrin, which gives a red color with iodine. Various intermediate forms are known.[1] In the endosperm of sweet and waxy-sweet varieties of maize Lampe and Meyers (1925) state that the first storage carbohydrate may appear in the form of liquid globules staining red with iodine. Within these globules, and also in cells without such globules, there then appear solid grains of starch, which stain blue in the sweet variety and red in the waxy-sweet.

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[1] For the composition of starch, see Géza-Zemplin (1911), Czapek (1913), Reichert (1913), Meyer (1913, 1920). For the structure of the starch granule, see the papers of Nägeli, Schimper, Meyer, Binz, Dodel, Salter, Kramer, and Sponsler. For the occurrence of starch, see Meyer (1895) and Winkler (1898). Starch is said not to occur in Phæophyceæ, Diatoms, Cyanophyceæ, fungi, and animals. Belzung (1887) and Eberdt (1891) deal with the origin of starch in chloroplasts and amyloplasts respectively. For accounts of Floridean starch see Schmitz (1882), Bruns (1894), O. Darbishire (1896), Henckel (1901), Kylin (1913), and Mangenot (1923*a*).

*Cellulose* is the chief constituent of the cell wall in most groups of plants. It is not often found in the pure state in the wall, other substances, notably lignin, ordinarily being present in physical or chemical combination with it. The proportion of pure cellulose may be as high as 90 per cent in cotton fiber, but in beech and oak wood it is as low as 35 per cent. Although chiefly supporting in function, cellulose is sometimes used as a reserve product. The hemicelluloses, or "pseudocelluloses," more often function in this capacity.

Closely allied to the celluloses are the pectins, which appear to be formed by the hydrolysis of the pectose of the middle lamella. Glycogen, a substance of great importance in animals, is found also in the Cyanophyceæ, myxomycetes, fungi, and bacteria. It may exist in the form of viscous or solid masses in the cytoplasm, or in colloidal solution in the vacuole. In these plants it appears to function much as starch does in higher plants. The many mucilages and gums which occur so widely in plant tissues are composed chiefly of carbohydrate materials, the former being condensation products of various sugars, and the latter these products together with complex acids (Onslow). Plant slimes may apparently arise in different cases as modifications of cell wall substance, within the cytoplasm, or at the boundary between the cytoplasm and the vacuole (Czapek; E. L. Smith, 1923). Sugars of several types are of especial importance in the metabolism of plants, and are frequently present as storage products.

**Proteins.**—Ergastic protein bodies are constantly being encountered in cytological study. These may be either crystalline or non-crystalline, and may lie in the cytoplasm, plastids, nucleus, or vacuole. In animal eggs the storage materials commonly occur in the form of "yolk globules," or "deutoplasm spheres," which consist for the most part of relatively complex protein compounds; globules of fat or oil are usually associated with them. In the eggs of gymnosperms, also, are found large globules or shapeless masses of albuminous reserves. The somatic cells of plants frequently contain many small scattered masses which stain intensely with nuclear dyes and strongly suggest the "chromidia" of certain animal cells (Chapter XII). Refractive "metachromatic corpuscles," composed of metachromatin, a nucleic acid compound, may occur in the vacuoles and cytoplasm of certain algæ, fungi, and Protozoa (Guilliermond); these are what A. Meyer calls volutin globules. Dangeard considers the metachromatin of these organisms to be identical with that in the vacuoles of Metaphyta.

Protein crystals occur widely in both plants and animals. They consist chiefly of albumins and globulins, and may be found in the cytoplasm, plastids, nucleus, or vacuole.[1] The best-known albumin crystals are those found in *aleurone grains*, which are ordinarily made up of both crystalline and amorphous protein elements. These grains occur in the endosperm, embryo, and perisperm of ripe seeds, being especially prevalent in such oily seeds as those of *Ricinus*, *Juglans*, and *Bertholletia*. In maize and wheat kernels they lie chiefly in the outermost layer of endosperm cells, though a few occur in the cells beneath. Aleurone grains differ considerably in color, form, and structure.[2] In many cases (*e.g.*, *Pisum*) the grain consists only of an amorphous substance. In other cases this ground substance encloses a rounded "globoid" (in grasses), a crystal of calcium oxalate (in certain Umbelliferæ), or a large angular albuminous "crystalloid." In *Myristica surinamensis* all of these elements occur in the same grain. The well-known aleurone grain of the deeplylying endosperm cells of *Ricinus* consists of a protein ground substance, a crystalloid, and a globoid composed of a double phosphate of calcium and magnesium together with certain organic constituents (Fig. 45).

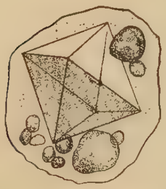

FIG. 45.—Aleurone grain from endosperm of *Ricinus communis*. (*After A. Meyer*, 1920.)

The development of the aleurone grain has been repeatedly studied, especially in *Ricinus*. It now seems clear that the early investigators (Maschke, Gris, Wakker) were correct in their statement that the grains appear in vacuoles as the seed dries out. The process has been more recently described by P. A. Dangeard (1919, 1920*ac*), P. Dangeard (1920, 1921*abc*, 1922*a*, 1923), and Mottier (1921). As the endosperm cell matures the vacuolar material passes through a reticular stage and breaks up into a number of small vacuoles, in which the gradually concentrating constituents differentiate as crystalloid, globoid, and ground mass (Fig. 6). According to Mottier, the albuminous material appears in the vacuole in the form of numerous small bodies, which then fuse to form one or more masses which become the crystalloid, near which is found the globoid. He has further interpreted the small bodies which first appear as permanent primordia which enter the vacuole from the cytoplasm, since in *Zea* and *Conopholis* he found such bodies apparently producing aleurone outside the vacuoles. This interpretation is rejected by the Dangeards, who claim that aleurone represents in all cases a stage in the evolution of the vacuolar system (see p. 44). This system, they claim, is autonomous. Therefore, whether the aleurone grains are produced by permanent primordia or as temporary differentiations in a permanent vacuolar system, the result would be of much importance to the student of the inheritance of aleurone characters. So far no genetic evidence has been found for the autonomous nature of aleurone-producing agencies (East and Hayes, 1911, 1915; Emerson, 1914, 1917). Reference has been made in previous chapters to the opinion of Meyer that chondriosomes and nucleoli are ergastic albuminous materials.

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[1] Protein crystals are treated at length by Meyer (1920). For nuclear crystals, see also Tischler (1921–1922).

[2] Hartig (1856), Maschke (1859), Gris (1864), Pfeffer (1872), Tschirch (1887), Wakker (1888), Lüdtke (1890), Guilliermond (1907*a*).

**Fats and Allied Substances.**—Fats and oils are of widespread occurrence as reserve materials in plants as well as in animals. In plants they are found commonly in seeds, spores, embryos, and meristematic tissues, and occasionally in differentiated vegetative parts. They are chiefly neutral, free fatty acid seldom being present in any considerable amount. They occur in the form of droplets in the cytoplasm, and occasionally in the nucleus also in animals. These droplets may often be very minute and numerous, but the claim that in some seeds they lie below the limit of visibility, or form a continuous phase (Policard and Mangenot, 1923*b*), the cytoplasm thus appearing optically homogenous ("oil-plasm"), needs further investigation.

It seems most likely at present that ordinary fat and oil droplets are elaborated directly by the cytoplasm rather than by special plastids or chondriosomes. The so-called "elaioplasts" which were long supposed to perform this function, as well as the "oil bodies" of liverworts, seem to be accumulations of albuminous and fatty materials rather than plastids (see p. 104). It is still claimed by Guilliermond and Mangenot (1923) that volatile oils have a chondriosomal origin, and Mangenot (1923*b*) attributes oil formation to phæoplasts in certain brown algæ.

Closely allied with ordinary fats is a group of substances known as *lipoids*. Those which contain phosphorus are called phosphatids, and the most familiar of these is lecithin. Lipoids occur so universally in protoplasm that their great physiological significance cannot be doubted; reference to this has been made in Chapter II. They probably form one of the most important phases of the colloidal protoplasmic system, and they frequently appear as small globules in the cytoplasm.

Waxes also bear a resemblance to fats in composition, and form waterproof coatings on many fruits, stems, and leaves.

**Crystals.**—Crystals of many kinds occur in the differentiated tissues of plants. They may lie in the cytoplasm, in vacuoles, and occasionally in the nucleus; they may be attached to or imbedded in the cell wall, and often the cells containing them are considerably modified in size and appearance. They are usually salts of calcium, the oxalate being especially prevalent. The bundles of needle-shaped crystals known as "raphides," and found so commonly in leaves, are composed of this salt (Fig. 46, *L*). According to E. L. Smith (1923), the raphides in orchids first arise in the middle of the vacuole of an enlarging cell, where they appear to be suspended by strands of a special substance which also forms a sheath about them. When they have attained practically their full size a yellow mucilage appears at the inner boundary of the protoplast and increases in amount until it fills the entire vacuole around the raphides. The spherical crystalline structures known as "druses" (Fig. 46, *C*) are also chiefly calcium oxalate, though they have a central mass of some more complex organic substance. The origin of the druse and its relation to the protoplast is at present a subject of controversy, Jeffrey's (1922) view that the druse is formed as a casing around the protoplast being opposed by Lloyd (1923), who contends that druses, more than one of which may be present in one cell, arise within the protoplasm and may later pass into the vacuole. Gaiser (1923) finds that the stellate crystal of *Anthurium* arises in the vacuole, and that after it comes to occupy nearly the whole cell the cytoplasm with the nucleus can still be seen surrounding it.

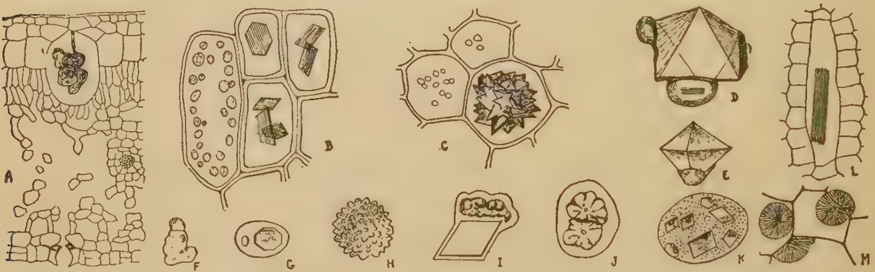

Fig. 46.—Crystalline and other ergastic materials in the cells of plants. *A*, cystolith in subepidermal cell of *Ficus* leaf. *B*, crystal cells in *Arctostaphylos*. *C*, druse in cell of *Rheum palmatum*. *D–K*, aleurone grains: *D*, *E*, from *Myristica; F*, from *Datura stramonium; G*, from *Ricinus communis; H*, from *Amygdalus communis; I*, from *Bertholletia excelsa; J*, from *Fœniculum; K*, from *Elœis guiniensis*. *L*, raphides in leaf of *Agave*. *M*, inulin crystals in preserved cells of artichoke. (*B–K after Tschirch.*)

The curious "cystoliths" in the *Ficus* leaf (Fig. 46, *A*) represent outgrowths of the cellulose wall heavily impregnated with calcium carbonate. In the cystoliths of certain Acanthaceæ the calcium may later disappear (Linsbauer, 1921). Crystals of silica are very abundant in the thickened walls of wood cells and in many other tissues, such as the outer portion of the *Equisetum* stem. In an earlier section reference was made to the protein crystals of aleurone grains, and to those frequently observed in the nucleus. Mirande (1923) states that the radiocrystals in the epidermis of white lily bulb scales consist of a phytosterol which he calls "liliostérine." The carbohydrate inulin, which often occurs in solution in the vacuole, appears as nodules of radiating crystals in tissues which have been preserved in alcohol (Fig. 46, *M*).

**The Cell Sap.**—The cell sap of plants occurs in vacuoles in the cytoplasm. The origin and general characters of vacuoles have already been discussed (p. 43), so that treatment here may be limited to the ergastic substances contained within them. The sap in young cells is ordinarily neutral or slightly alkaline in reaction (Dangeard), but it soon becomes acid, owing to the accumulation of organic acids (malic, formic, acetic, oxalic, etc.) and their salts, together with certain aromatic compounds, such as tannin. Since most of these substances are in molecular or colloidal solution, the sap is usually homogeneous in appearance. Analyses have shown that the following elements and classes of compounds occur in such saps: magnesium, aluminium, sodium, potassium, calcium, manganese, iron, nitrogen, phosphorus, sulphur, chlorine, iodine; organic acids (oxalic, malic, citric, acetic, tartaric, formic, etc.); alcohols; carbohydrates (dextrose, fructose, lactose, inulin, etc.); slimes; glucosides; anthocyanin and soluble yellow pigments, most of which exist in the form of glucosides; amides (glutamin, asparagin); alkaloids; albumins; certain enzymes; tannins; and a variety of other aromatic compounds (see A. Meyer, 1920).

Nearly all of the red, blue, and purple colors of flowers, fruits, and other plant parts are due to anthocyanin pigments dissolved in the cell sap. These pigments are red in an acid medium and blue or violet in an alkaline one, though these colors may be masked by other pigments in the sap or plastids. The yellow flavone and flavonol pigments are widely distributed in the cell sap of plants, but they occur in such dilute solution that they do not give a noticeable color to tissues except in rare cases (*e.g.*, *Antirrhinum*). Yellow color in plants is usually due to plastid pigments.[1]

Frequently the cell sap contains visible solid or fluid particles in suspension, and these may be so numerous as to give the sap a milky appearance. The *latex* found in special cells or vessel systems in certain plants is a sap which contains a great variety of substances in solution, together with suspended droplets or granules of oils, tannins, gum, starch, resin, caoutchouc, and other compounds. As familiar examples may be cited the juices of the rubber tree, dandelion, milkweed, and poppy.[2]

Under certain circumstances organic and inorganic substances dissolved in the cell sap may crystallize or precipitate. This may result from an increase in the concentration of such substances beyond the saturation point, often because of a decrease in the amount of solvent, as in drying seeds, or to the appearance of some other compound which precipitates them. Instances of this are seen in the raphides and aleurone grains described above. Dangeard has shown that metachromatin existing in colloidal solution may precipitate as "metachromatic corpuscles," or "endochromidia," when treated with certain fixing and staining reagents. In certain cases these are visible in living cells.

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[1] For accounts of plant pigments, see Onslow (1923) and literature there cited.

[2] For accounts of such saps, see Czapek (1913) and Meyer (1920).

Not only does the cell sap serve as a reservoir of water and nutritive materials and a depot for certain by-products, but it is undoubtedly the medium of many reactions of importance in the life of the plant. Its rôle in maintaining turgor is also noteworthy. Cell sap is ordinarily regarded as of relatively little importance in animals, but if the Golgi material should be shown to be homologous with the vacuolar material of plants, such a view would obviously need revision.

**Conclusion.**—In conclusion it will be well to recall the point stressed at the opening of the chapter, namely, the impossibility of distinguishing sharply between "living" and "non-living" components in protoplasm. The *living system* comprises all the *active constituents*. Ergastic substances are therefore to be thought of simply as the ill-defined group of materials which at any given moment are taking little or no part in the operation of the living system, but which become parts of that system when for any reason they become active.

# CHAPTER IX

## SOMATIC MITOSIS

In view of the fact that the growth and differentiation of protoplasm, the reproduction of the individual, and the phenomena of heredity are now known to be intimately bound up with reactions involving the nucleus, it is clear that a detailed knowledge of the process of nuclear multiplication by division is prerequisite to a solution of many outstanding problems. The division in nearly all cases is accomplished by a complicated series of changes known as *mitosis*, or *karyokinesis*, whereby the chromatic nuclear substance, in the form of individualized units, or *chromosomes*, is apportioned to the daughter nuclei with great precision. In the present chapter will be described the process of mitosis as it occurs in the development of the body, or *soma*, particular attention being given to the behavior of the chromosomes. The account will be completed in Chapter XI, which will deal more at length with the achromatic figure, and with the cytoplasmic division which usually accompanies the division of the nucleus.

**Preliminary Sketch of Mitosis.**—The main steps in a typical case of somatic mitosis in plants may be briefly outlined as follows (Fig. 47):

The karyotin of the metabolic ("resting") nucleus, as described in Chapter IV, exists in the form of a more or less irregular *reticulum*. As the process of mitosis begins, this reticulum resolves itself into a definite number of slender threads (*spiremes*) which represent *chromosomes*. These are usually distinct from one another, though in some cases they seem to be arranged end-to-end in a more or less continuous spireme, which later breaks up into independent chromosomes. The thread-like chromosomes split longitudinally throughout their entire length. The double threads so formed then undergo a progressive shortening and thickening, and become the conspicuous split chromosomes seen at later stages.

The nuclear membrane now shrinks and disappears, and the nuclear region is seen to be occupied by a viscous, hyaline substance. This takes the form of a spindle-shaped mass, or *achromatic figure*. In fixed preparations numerous fine fibrils appear in the hyaline mass, and as the double chromosomes become regularly arranged in its equatorial plane these *spindle fibers* are observed to extend from definite points on the split chromosomes toward the poles of the figure. This stage is known as the *metaphase;* all the steps leading up to it, beginning with the initial changes in the resting reticulum, constitute the *prophase.*

The halves of each longitudinally split chromosome now pass to opposite poles of the achromatic figure, where they form two groups with a mass of spindle substance extending between them. The period during which the daughter chromosomes are thus moving apart is known as the *anaphase.* The two groups of chromosomes now reorganize as daughter nuclei, in each of which they form a reticulum like that of the mother nucleus. This reorganization period is called the *telophase.* During the telophase of division in cellular tissue the new cell membrane is differentiated in the equatorial plane of the spindle substance between the nuclei. The nucleolus ordinarily disappears during the late stages of the prophase, new nucleoli differentiating in the daughter nuclei in the telophase. The period between two rapidly successive mitoses is called the *interphase.*

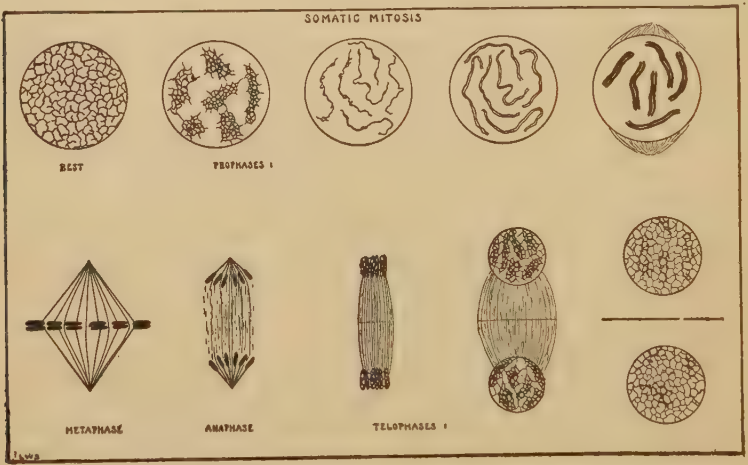

FIG. 47.—Diagram of somatic mitosis in a plant with large chromosomes.

Mitosis in animals (Fig. 48) is closely similar to that in plants as regards the behavior of the chromosomes. It usually differs, however, in certain features of the achromatic figure and in the mode of cytoplasmic division (cytokinesis) following the division of the nucleus. During the prophase the centrosome, if not already double, undergoes division, the daughter centrosomes then moving apart. Each of them occupies the center of a semi-solid region, or *aster,* with conspicuous "astral rays," and between them is a *central spindle* with fine fibrils; all these structures together make up the *amphiaster.* The centrosomes, surrounded by their asters, reach opposite sides of the nucleus and remain as the polar foci of the achromatic figure through the metaphase, anaphase, and telophase.

Cytokinesis is commonly brought about in animals by a cleavage furrow which grows inward from the periphery of the protoplast, rather than by the differentiation of a plate-like wall as in plants.

Although the mitotic process in animals usually differs from that in plants in the two above points, the distinction is by no means a sharp one. Centrosomes are regularly present in many algæ and fungi, and cytokinesis by furrowing also occurs in certain cells in both the lower and the higher plant groups. The essential point to be borne in mind is that the significant feature of mitosis—the division of the chromosomes and their distribution to the daughter nuclei—is fundamentally the same in both plants and animals.

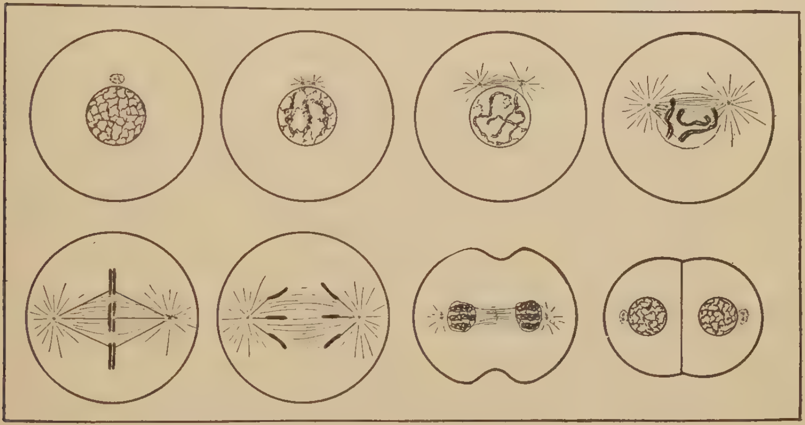

Fig. 48.—Diagram of a typical case of mitosis in an animal.

**Duration and Periodicity of Mitosis.**—The duration of the various phases of mitosis has been studied in a few instances. Strasburger (1880) and de Wildeman (1891) found the entire process to occupy several hours in the stamen hair of *Tradescantia.* M. and W. Lewis (1917) give the following figures for mesenchyme cells of the chick growing in tissue cultures at 39°C.: prophase, 5 to 50 minutes, usually more than 30; metaphase, 1 to 15, usually 2 to 10; anaphase 1 to 5, usually 2 to 3; telophase up to cytokinesis, 2 to 13, usually 3 to 6; telophasic reconstruction of daughter nuclei, 30 to 120; total, 70 to 180 minutes. In similar cultures of choroidal cells from the eyes of chick embryos and cartilage cells from adult fowls, Strangeways (1922) finds the process to be more rapid at the same temperature, complete division being accomplished in from 23 to 65 minutes, with the average at about 34 minutes. In *Sphacelaria fusca,* a brown alga, growing at 17 to 18°C., W. Zimmermann (1923) observes that the prophase occupies 10 minutes, the metaphase 7, the anaphase 4, and the telophase 9; total, 30 minutes. Laughlin (1919) has made an elaborate

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statistical study of fixed preparations made from root tips of the common onion (*Allium cepa*) growing at different temperatures. His results may be summarized approximately as follows. At 10°C.: metabolic or resting stage, 195 minutes; prophase, 88; metaphase, 1.4; anaphase, 3; telophase, 4.6; total, 292; total, excluding rest, 97. At 20°C.: rest, 159; prophase, 74; metaphase, 1; anaphase, 2.5; telophase, 4; total, 241; total, excluding rest, 81. At 30°C.: rest, 33; prophase, 55; metaphase, 0.3; anaphase, 1; telophase 1.5; total, 91.5; total, excluding rest, 78. Laughlin finds that each stage shows a characteristic velocity reaction to temperature increments, and that these approximate the expectations based on Van't Hoff's law for the velocity of simpler chemical reactions.

With regard to periodicity, it is a well-known fact that nuclear and cell-divisions frequently show a marked tendency to occur only at certain hours of the day or night. Certain algæ, for example, undergo division only during a comparatively short period in the night. Several investigators have found distinct periodic fluctuations in the number of mitoses observable in sections of meristematic regions of higher plants growing under uniform experimental conditions, but a full explanation of their somewhat divergent results cannot at present be given. Kellicott (1904) reported that *Allium* roots showed division maxima at 1 and 11 p.m., and minima at 7 a.m. and 3 p.m.; and further that the rate of elongation showed maxima and minima corresponding closely to the division minima and maxima respectively. In *Pisum* roots Friesner (1919, 1920) found three division maxima, at 1 p.m., 5 p.m., and 5 a.m.; and three minima, at 11 a.m., 3 p.m., and 9 p.m. In *Allium* he found apparently four or five periods per day. Friesner, like Kellicott, noted a distinct correlation between maximum elongation and minimim division; and he pointed out that such phemomena depend not solely on the hour of the day, but on the length of time after germination. Karsten (1915, 1918) found no division rhythm in the roots of *Vicia* and *Zea*, but in young shoots he found a distinct maximum at 11 p.m. in *Pisum* and at 4 a.m. in *Zea*. In *Pisum* roots Stålfelt (1919, 1921) found a division maximum between 9 and 11 a.m. and a minimum between 9 and 11 p.m., but no daily elongation periods. Many experiments have shown that, although the periodicity in such cases may be altered by changing the environmental conditions, there is a decided tendency to maintain the habitual rhythm. This indicates the action of both external and inherent factors, whose respective rôles in determining the observed results have not been fully analyzed (see Stålfelt, 1921).

**The Behavior of Large Chromosomes in Somatic Mitosis.**—In the following account we shall depart from the order usually followed in descriptions of mitosis. Instead of commencing with the resting nucleus and tracing the steps leading to the formation of two daughter resting nuclei, we shall begin the description with the fully formed chromosomes as they appear in the metaphase and follow them through anaphase, telophase, resting stage, and prophase to the next metaphase, when they are again clearly seen. This is done in order that the account of the telophasic transformation of the chromosomes to form a resting reticulum and the prophasic condensation of the latter to form chromosomes may be given without interruption, which seems advisable in view of the nature of certain questions which are later to be discussed in the light of chromosome behavior.[1]

*Metaphase.*—As the split chromosomes become arranged in the median plane of the achromatic figure their double nature is clearly evident (Fig. 49, *A*). The two halves may be very closely appressed, and in the case of long chromosomes may be somewhat twisted about each other. Often they show small connecting strands or anastomoses; these may be due to a coherence of the viscid bodies following a close contact during the late prophase, or they may originate at a much earlier stage. The spindle fibers which appear in the fixed achromatic substance extend toward the poles from a definitely localized point on each chromosome. In *Vicia* this point is at the middle of the two long chromosomes and at the ends of the ten short ones (Fig. 63). In *Crepis virens* the fiber insertion is terminal in the short and medium-sized chromosomes, and intermediate in the long ones (de Litardière, 1923*b*) (Figs. 64, *B*; 180; 181). Chromosomes with terminal insertion are said to be *telomitic;* those with the insertion elsewhere are *atelomitic.*[2] The insertion points of all the chromosomes lie in a single plane with the chromosome halves superposed (one-half toward each spindle pole); those portions of long chromosomes to which no fibers are attached may extend in various directions with no regular arrangement.

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[1] This description is based on the author's accounts of somatic mitosis in *Vicia faba* (1913) and *Tradescantia virginiana* (1920*a*). In these papers, especially in the first, there is presented a more extensive comparison of the results of earlier investigators than can be given here. Comparative studies have shown that in its general features the present description is widely applicable to mitotic phemonema in plants and animals with large chromosomes. Closely conformable to it are the accounts of de Litardière (1921*ab*) for *Podophyllum* and certain ferns, Kuwada (1921) for *Vicia*, and Overton (1911, 1922) for *Podophyllum*, although the last named differs in certain important points to which attention will be directed. A rather different interpretation of the structural changes undergone by the chromosomes, originally suggested many years ago, has recently been revived in a number of papers based on researches with new microtechnical methods. We have elected to deal first with the aspects observed in material treated by the usual methods and widely reported in the literature, leaving a consideration of the results of the above-mentioned researches and other controverted points to a later section dealing particularly with the structure and division of chromosomes. A useful list of works on mitosis in angiosperms is given by Picard (1913). Ruys (1925) lists the angiosperm genera in which nuclear studies have been made, with a bibliography of about 1,200 titles.

[2] This feature was first carefully studied in insect spermatocytes by McClung, Carothers, Wenrich, and others, and was later shown in somatic cells also. We shall later refer to its bearing on the question of chromosome organization. The terms were introduced by Carothers (1917).

*Anaphase.*—The daughter chromosomes (the halves of the split chromosomes seen in the metaphase) begin to separate, first at the points of fiber insertion, and gradually move away from the equatorial plane toward opposite poles of the achromatic figure (Fig. 49, *B-D*). Owing to the different locations of their insertion points and the various positions occupied by their free ends, the chromosomes may now assume a number of peculiar shapes. In the case of long chromosomes the portions to which fibers are attached may have reached the poles before the other portions have separated at the equatorial plane. As soon as they become entirely free from one another they rapidly draw apart and contract into two compact groups, which are often actually farther apart than were the poles of the achromatic figure in the metaphase. The groups are frequently so dense that the individual chromosomes can be distinguished only with difficulty or not at all, and the naturalness of the appearance

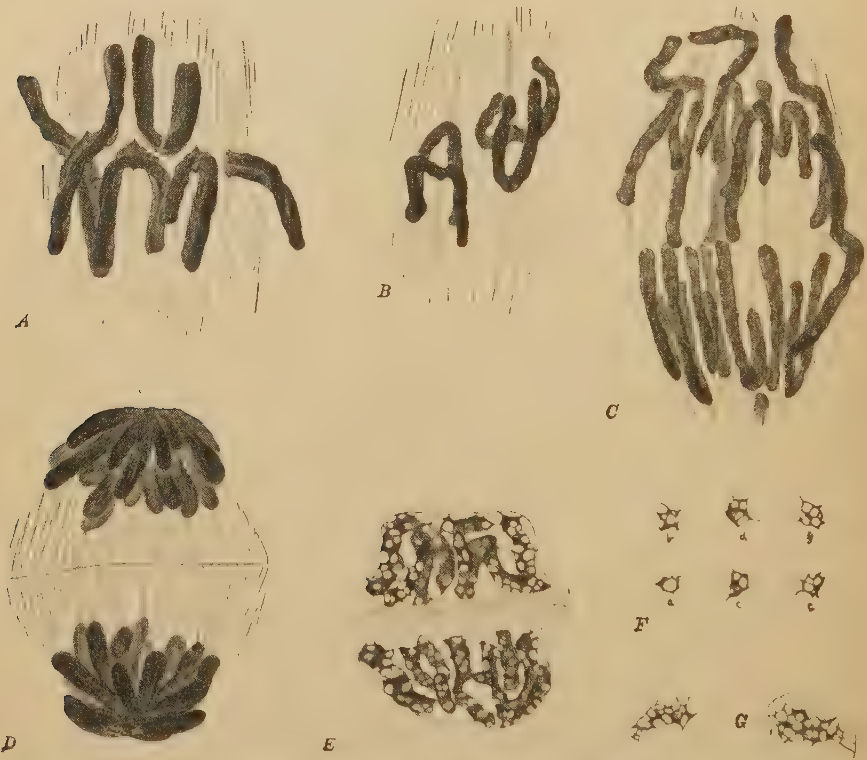

Fig. 49.—Somatic mitosis in *Tradescantia virginiana*. *A*, metaphase; *B–D*, anaphase; *E–G*, telophase. At *F* are shown transverse sections of chromosomes in the stage shown at *E*. (*After Sharp*, 1920.)

has frequently been doubted. Although it is probable that poor fixation may serve to accentuate the compactness in certain cases, there can nevertheless remain no doubt that, in general, a very close grouping of the chromosomes occurs naturally. With this stage (the *tassement polaire* of Grégoire and Wygaerts, 1903) the anaphase ends and the telophase begins.

Throughout the anaphase the region between the separating groups of chromosomes is occupied wholly by the hyaline achromatic spindle substance, in which longitudinal fibrils appear with varying degrees of distinctness depending on the method of fixation employed.

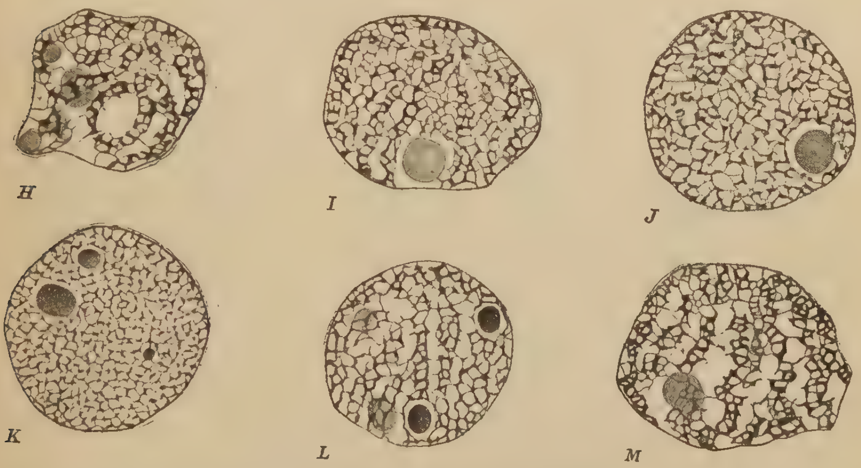

FIG. 50.—Somatic mitosis in *Tradescantia virginiana:* late telophase (*H*, *I*), interphase and resting stage (*J*, *K*), and early prophase (*L*, *M*). × 1900. (*After Sharp*, 1920.)

*Telophase.*—During the telophase the two groups of chromosomes reorganize the two daughter nuclei (Figs. 49, *E-G*; 50, *H*, *I*). The changes undergone by large chromosomes in this period are essentially as follows. In each group the chromosomes become less closely packed, clear spaces being visible between them. As they thus move slightly apart they cohere at various points, where their substance becomes drawn out to form anastomoses. There can be no doubt that connections between the chromosomes of the reorganizing telophase nucleus originate in this way, especially in cases showing a decided *tassement polaire*, as in *Vicia*. It is also evident, as several investigators[1] have shown, that other anastomoses may grow out from the chromosomes in the manner of pseudopodia, for they appear between small chromosomes which have never been closely packed. Moreover, Lewis and Lewis

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[1] Boveri (1904), Strasburger (1905*a*), Dehorne (1911), Lundegårdh (1912*a*), Gates (1912), Müller (1912), de Litardière (1921*b*).

(1924) state that active chromosomal pseudopodia can be seen in living cells in tissue cultures.

Changes occurring within the chromosomes now result in the appearance of a more or less distinct internal structure. This usually takes place at about the time the chromosomes begin to loosen up as already described, but in some cases the structure is evident in the anaphase or even in the metaphase. It now seems probable that the structure appearing in the telophase is not formed wholly anew at that time, but is present in some degree throughout most if not all of the mitotic cycle, often being obscured during late prophase, metaphase, and anaphase because of certain staining reactions.

The transformation occurring in the telophase chromosomes has been variously described, as will be shown at some length later in the chapter. For some time one of the most prevalent interpretations has been the following. Within each chromosome, both along the axis and near or against the periphery, there appear circular or elongated areas which soon become very sharply delimited and relatively achromatic, or colorless. The origin and nature of these "alveoles" are little understood; it has been thought that they represent either droplets of a newly elaborated substance (Tischler), or regions from which a distinct chromatic component of the chromosome has withdrawn, leaving an achromatic substratum visible (de Litardière). As the nucleus enlarges, the alveoles increase in size and become more irregular in form, while the chromatic portions gradually become more attenuated, so that each chromosome appears as an irregular net-like body joined to its neighbors by fine anastomoses. The process continues, the chromosomes forming together a more and more uniform karyotin reticulum, in which, however, the constituent chromosomes can be distinguished until a very late stage.

The fate of the achromatic alveoles during these telophasic changes and their relation to the karyolymph are important questions which it is very difficult to answer. It has seemed to some investigators (Tischler, Sharp) that they break through the chromosomal boundary and become continuous with the karyolymph, the nucleus thus being a continuous mass of hyaline substance with a continuous chromatic reticulum imbedded in it (Fig. 51, *A*). This is also the view of certain authors who believe the chromatic material to have the form of spirals (*e.g.*, Kaufmann, 1926). Some have thought that all of the karyolymph has such an origin; in fact, Tischler (1921–1922) speaks of its periodic secretion by the chromosomes. He, with Gates (1909*a*) and others, have thought it probable that the nuclear membrane forms by precipitation where the karyolymph comes in contact with the cytoplasm. Others have thought it more probable that the karyolymph must come mainly from another source, since many chromosomes show no alveolation. De Litardière (1921*b*) is of the opinion that the karyolymph of the mother nucleus occupies the spindle region during mitosis and moves in between the chromosomes of the daughter nuclei after the *tassement polaire*, additional fluid being contributed later by the cytoplasm. This is in harmony with the growing view that the achromatic spindle substance is chiefly the karyolymph. If it is true that the alveoles break through the chromosome boundary, it would thus appear probable that the achromatic substance, which seems to be largely of nuclear origin, is derived in part from the chromosomes themselves.

That the achromatic chromosomal substance, whether in the form of "alveoles" or not, does not actually mingle with extra-chromosomal fluids is a view for which favorable evidence is steadily accumulating. According to this interpretation, the chromosome in the telophase, and possibly in all other stages, consists of an achromatic matrix definitely delimited from the karyolymph, and a chromatic component which forms the reticulum. Thus in the late telophase and metabolic stages each chromosome is represented not solely by a portion of the karyotin reticulum, but by a portion of the colorless nuclear substance in addition (Fig. 51, *B*). Another interpretation possible for some cases is that the nucleus contains nothing but the chromosomes, which remain in close contact as the telophasic transformation proceeds; adjacent chromosomes may become continuous in both chromatic and achromatic parts, or they may be separated by membranes visible in the case of "karyomeres," or "chromosomal vesicles" (Fig. 60, *A*, *B*). The nuclear boundary in such a case would be constituted by the surfaces of the outermost chromosomes of the group, and there would be no fundamental distinction between karyolymph and achromatic chromosomal substance, the former arising by a swelling of the latter (Fig. 51, *C*). According to

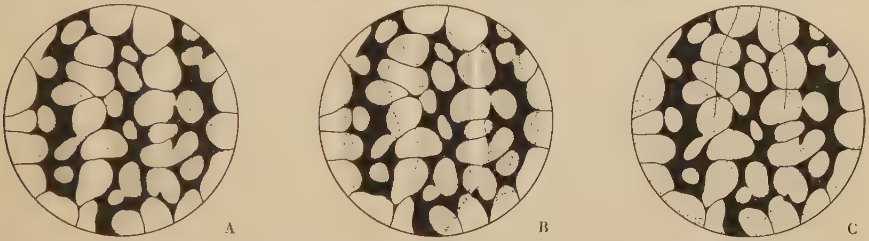

FIG. 51.—Diagrams illustrating various theories regarding the structure of the nucleus in the metabolic or resting stage. The chromatic chromosomal substance is shown in black, the achromatic chromosomal substance by stippling, and karyolymph of extra-chromosomal origin in white. In *A* the achromatic chromosomal element is seen mingling with extra-chromosomal karyolymph; in *B* these two substances remain distinct; in *C*, the "karyolymph" is regarded as being composed wholly of achromatic chromosomal substance. In the upper half of *C* the chromosomes are shown separated by persisting membranes; in the lower half no such membranes are present. To accord better with the chromonema hypothesis the black portions should be shown more slender and filament-like (compare Fig. 58). The distinctness of the individual chromosomes is of course exaggerated.

the interpretation of Robyns (1924), the interphase nucleus in root cells has no special membrane in addition to the chromosome surfaces. Early in the prophase a fluid which had been absorbed by the chromosomes in the preceding telophase is disengaged from them and becomes the karyolymph. Where this touches the cytoplasm a membrane is then formed. Much light should be thrown on these questions by studies on small chromosomes which do not undergo alveolation.

As already stated, the internal changes which result in the transformation of the chromosomes into a reticulum, and which as a rule are not apparent until the telophase, may be evident during the anaphase. In *Allium*, for instance, Merriman (1904), Lundegårdh (1910, 1912*b*), and Němec (1910*a*) all report that they begin at this time. Even more striking is the case of *Trillium* (Grégoire and Wygaerts, 1903), in which the unusually large chromosomes may show internal structure as early as the metaphase (Fig. 56, *A*). Indeed, it seems that such large chromosomes as those of *Trillium* and *Paris quadrifolia* may show the differentiation into chromatic and achromatic regions throughout the nuclear cycle.[1]

Special notice should be taken of the view of several investigators[2] that the alveolation in the telophase is median and results in a partial or complete longitudinal splitting of the chromosome, which then remains through the interphase as a double structure and develops directly into the divided chromosome seen at the succeeding metaphase. Others[3] have opposed this interpretation chiefly on the basis of detailed examination of the arrangement and fate of the telophasic alveoles, together with a significant change which occurs in the following prophase, to which attention will later be called. It is true that a median arrangement of clear spaces frequently gives the telophase chromosome a double appearance, especially if it is slender, but this appears to be a special case of a more general transformation, which in larger chromosomes bears no necessary relation to the median region. In Figs. 49 and 50 it is seen that the clear spaces occupy every conceivable position (see especially the transverse sections of telophase and prophase chromosomes in Figs. 49, *F* and 52, *N*). Through the process of telophasic alveolation the chromatic chromosomal material becomes an irregular reticulate cylinder with nothing that can properly be called a longitudinal split.

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[1] This appears to be the case in preparations of *Trillium* now being studied by the author.

[2] Lundegårdh (1910, 1912) on *Vicia* and *Allium;* Fraser and Snell (1911) and Fraser (1914) on *Vicia;* Frisendahl (1912) on *Myricaria;* Digby (1910, 1919) on *Galtonia* and *Osmunda;* Carruthers (1921) on *Hyacinthus*. Telophasic splitting is also reported by Tschenzoff (1916) and Tannreuther (1923) for *Euglena*, and by Robertson (1920) for certain insects.

[3] Grégoire (1912) on *Galtonia, Trillium,* and *Allium;* Gates (1912) on *Œnothera;* Sharp (1913, 1920) on *Vicia* and *Tradescantia;* Kuwada (1921) on *Vicia;* de Litardière (1921*b*) on several ferns; Overton (1922) on *Podophyllum;* Martens (1922) on *Paris*, and others. Prophasic splitting was described in many cases before the telophase interpretation was suggested.

Opposed to the foregoing interpretation of the telophasic transformation as a differentiation then occurring in the chromosome, and showing itself as an "alveolation," is another view according to which the relatively colorless areas are not actually alveoles, but regions in which the staining reaction of an achromatic chromosomal substratum begins an alteration which, when completed, reveals the presence of a chromatic component persisting throughout most if not all of the nuclear cycle as a zigzag or spiral filament, the *chromonema.* The failure of this chromonema to appear at certain stages in many chromosomes is attributed to a periodic chromaticity of the matrix in which it lies. Accordingly, the chromatic reticulum of the ensuing interphase and metabolic stage is regarded not as a group of united elementary chromosomal reticula, but rather as a complicated system of more or less individualized filaments. This interpretation, for which increasingly cogent evidence is being brought forward, will be considered in greater detail later in the chapter.

*Interphase.*—The telophase merges imperceptibly into the interphase (Fig. 50, *J*). In rapidly growing tissues, such as the meristem of the root tip, the mitoses often succeed one another so rapidly that the telophasic changes may not proceed far enough to obscure the limits of the chromosomes in the reticulum before the changes of the ensuing prophase begin. In such tissue it is not always possible to tell whether a given nucleus will undergo further telophasic changes or will at once enter upon the prophase. Such interphasic nuclei develop nucleoli, but chromocenters (in species which have these bodies) are usually not formed until a more advanced stage.

*Metabolic or Resting Stage.*—In slowly growing tissue the successive mitoses do not follow one another with very great rapidity, and the telophasic changes are carried on until the condition characteristic of typical nuclei is reached; the interphase here becomes the prolonged "resting" stage (Fig. 50, *K*). The foregoing description of the telophase enables us to evaluate the claim frequently made that the chromosomes at this time are "resolved into granules" which are scattered over a supporting framework through the metabolic stage. The "framework" and the "granules" are seen to be respectively the attenuated and the remaining denser portions of a continuous karyotin reticulum, as has been shown in Chapter IV. In the reticulum the limits of the constituent chromosomes usually become wholly invisible, although it is known that in certain cases such nuclei, if properly sectioned and stained, may reveal heavier and lighter areas in the reticulum which represent respectively the chromosomes and the regions of anastomosis between them. The importance of these facts will be apparent in the treatment of the individuality of the chromosomes in the next chapter.

*Prophase.*—The first indication that the prophase changes have begun is seen in the breaking down of the reticulum in certain regions (Figs. 50, *L*, *M*; 52; 53). In the case of nuclei which show heavier and lighter areas in their reticula this breaking down occurs along the light portions. In view of what has been said concerning the origin of the reticulum in the telophase, it is apparent that its breaking up in the prophase represents in such cases the separation of the constituent chromosomes from each other along the lines of their telophasic union; and it has been inferred that a similar interpretation applies to those nuclei in which the reticulum is perfectly uniform, or in which the nuclear material assumes more irregular forms. In this way there are developed from the reticulum a number of more or less distinct units, which, in view of their subsequent behavior, are known to be the chromosomes (Fig. 50, *L*, *M*). That these units are essentially the same as those which went to make up the reticulum in the preceding telophase seems highly probable; there can be little doubt on this point when the interphase is of short duration.

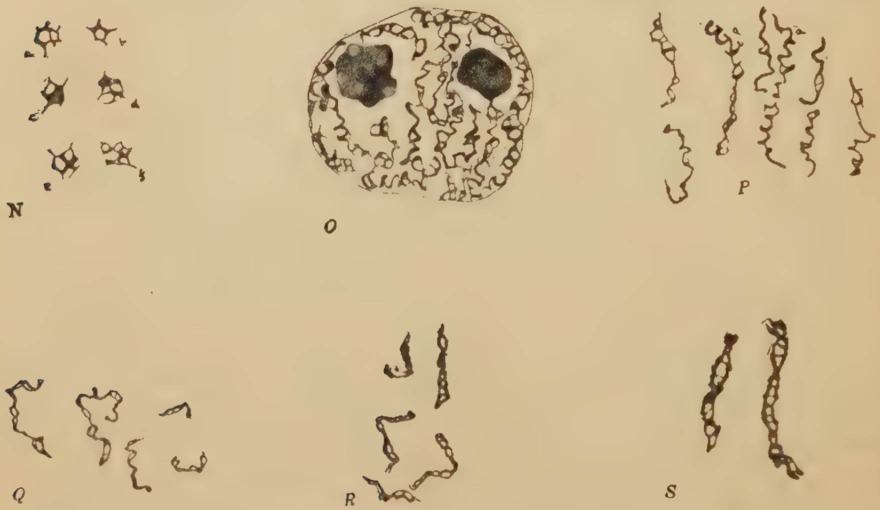

Fig. 52.—Somatic mitosis in *Tradescantia virginiana;* various stages of the prophase. At *N* are shown transverse sections of chromosomes in the stage shown in Fig. 50, *M*. (*After Sharp*, 1920.)

The chromatic material of each reticulate unit (chromosome) now gradually condenses in a very irregular fashion. The thinner regions bounding the achromatic spaces become broken down, and the thicker portions remain as a very irregular zigzag thread of uneven thickness, which soon begins to straighten out (Fig. 52, *P*). At the same time the material composing the thread becomes more evenly arranged throughout its length, so that it eventually takes the form of a single slender filament.

All of these changes—condensation, straightening, and equalization in thickness—may be seen going on simultaneously in different chromosomes of the same nucleus, or even in different portions of a single chromosome.

The formation of the slender prophase chromosomes from the reticulum in the above manner was first described in detail by Grégoire and Wygaerts (1903) and Grégoire (1906), and new cases have since been added. The above writers, together with Němec (1910), Digby (1910), and Müller (1912), believe that the reticulate chromosome may also condense directly into a slender thread without passing through the pronounced zigzag stage described above. Later researches have shown that such direct condensation probably does not occur in very large chromosomes, but that it is the regular method followed in slender or small chromosomes (de Litardière, 1921*b*). In certain amphibians, insects, and other animals Janssens (1901), Wilson (1912), and others have described the "spinning out" of the karyotin as contorted threads from the "chromatic blocks" in the early prophase.

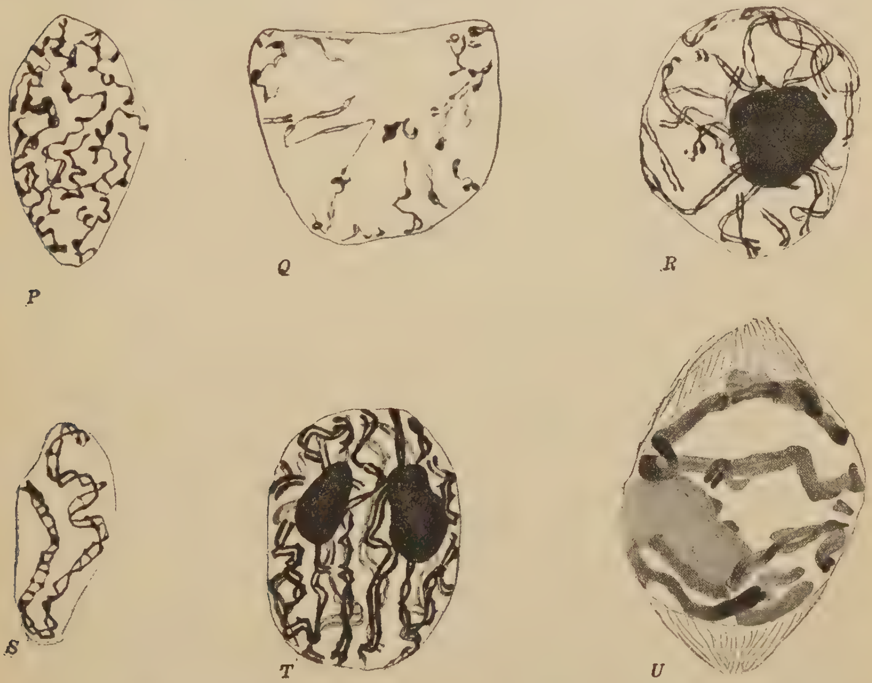

FIG. 53.—Somatic mitosis in *Vicia faba;* prophases. Stages *P*, *Q*, and *S*, correspond with *P*, *Q*, and *S* of Fig. 52. (*After Sharp*, 1913.)

A number of writers have interpreted the slender chromatic filament as a more or less regular and continuous spiral *chromonema,* which arises within the chromosome in the telophase or earlier, persists through the metabolic stage, and emerges from the chromosome in the following prophase (Bonnevie, 1908, 1911; Vejdovský, 1912). This is one of the important matters to be considered in a later special section.

The question of the achromatic chromosomal material arises again mat this point. Those who have thought that the achromatic chromosomal substance becomes continuous with the karyolymph in the telophase have, as a rule, regarded the chromosome as being only the chromatic filament, and have not figured a distinct achromatic component (Fig. 57). Others distinguish such a component from the karyolymph, and speak of the formation of the chromatic filament within an achromatic sheath or matrix (Fig. 58). On the theory that the nucleus is composed only of chromosomes, the karyolymph itself would be regarded as such a matrix.

The *longitudinal splitting of the chromosomes* now takes place. The finer details of this process, which are comparatively little understood, will be discussed in a later section. In some way the slender filaments become more or less completely double throughout their length (Figs. 52, 53). Not all of them necessarily undergo the change at the same time. In the same nucleus the processes of filament formation, straightening, equalization of material, and splitting may be occurring simultaneously; only in a given region of a filament do they follow in definite sequence. Furthermore, as soon as the filaments become equalized, they at once begin to shorten and thicken, so that if splitting is delayed it may occur in somewhat heavier threads. The shortening and thickening continue, giving the "thick double spiremes" so conspicuous in late prophase nuclei. The split may at this period become obscured by the close association of the halves, especially after poor fixation, but suitable methods reveal its presence.

The foregoing constitutes a second line of evidence against the view that telophasic alveolation represents true chromosome splitting. The reticulate condition developed by telophasic alteration and retained through the metabolic stage does not pass directly into the double spireme condition of the prophase; but rather, by a peculiar process in which most if not all of the telophasic openings in the reticulum are lost, the reticulate chromosome takes the form of a single thread in the prophase, and in this thread the split develops.

In the final stages of the prophase the nuclear membrane disappears as the achromatic figure makes its appearance. Usually the nucleus contracts at this time, so that the thick double chromosomes become very closely packed together; the membrane then disappears and the chromosomes loosen up as an irregular group. The hyaline nuclear substance in which they lie forms the achromatic spindle figure, in which fixation reveals fine longitudinal fibrils. The double chromosomes quickly become arranged with a certain portion of each of them lying in the equatorial plane of the achromatic figure, where their halves lie superposed. From these portions fibrils extend toward the poles, as described in the paragraph on the metaphase.

It should be added that it is frequently stated in descriptions of mitosis that the chromosomes split during the metaphase, after they have become arranged in the achromatic figure. Although direct evidence does not enable one to deny that the split in some cases may develop in the very late prophase or the metaphase, it is true that suitable methods have frequently revealed the inception of such supposedly late splitting at much earlier stages. As has been pointed out above, the early split often becomes obscured during the later prophases owing to the shortening and thickening of the chromatic threads, and again becomes conspicuous only after the metaphase figure has been established. This is notably the case with small chromosomes (de Litardière, 1921*b*).

**The Behavior of Slender and Small Chromosomes in Somatic Mitosis.** To illustrate the changes undergone by slender and small chromosomes in mitosis certain examples from the work of de Litardière (1921*b*) on the ferns may be selected. In these plants it is found that the telophasic transformation of the chromosomes (*catachromasis:* Vejdovský, 1907) occurs in four general modes, each of which is accompanied by a corresponding mode of prophasic transformation (*anachromasis*). These show no correlation with taxonomic position; and, since they merge into one another, the features of each are helpful in accounting for features of the others.

The first mode is found in species with large chromosomes, such as *Hymenophyllum tunbridgense*, *Leptopteris superba*, and *Osmunda cinnamomea*. Here the course of events is in all essential points the same as in *Vicia faba* and the other plants described in the foregoing section.

A second mode characterizes very slender chromosomes, such as are found in *Pteris cretica*, *Polypodium aureum*, and *Ceratopteris thalictroides* (Fig. 54, *E-G*). Here the chromosomes undergo no telophasic alveolation, but are drawn out into filaments connected by anastomoses to form the interphasic reticulum. In the prophase the anastomoses are retracted and the chromatic substance is concentrated directly into slender crooked threads which split and then thicken.

A third mode, intermediate between the two just described, occurs in *Blechnum occidentale*, *Trichomanes radicans*, and *Marattia fraxinea*, which have chromosomes of intermediate thickness (Fig. 54, *A-D*). In the telophase some of the chromosomes show narrow axial alveoles, while others remain unalveolized as simple filaments; all of them are connected by anastomoses to form the reticulum. In the prophase each of the chromosomes becomes an irregular simple thread, the alveolized ones indirectly as in the first mode, and the unalveolized ones directly as in the second. The split develops in these simple threads, but it may be obscured in the thick threads of the later prophase and not reappear until the metaphase.

The fourth and simplest mode is found in *Azolla* and *Salvinia*, which have very small chromosomes (Fig. 54, *H-L*). These chromosomes are round or ovoid bodies which undergo no structural transformation other

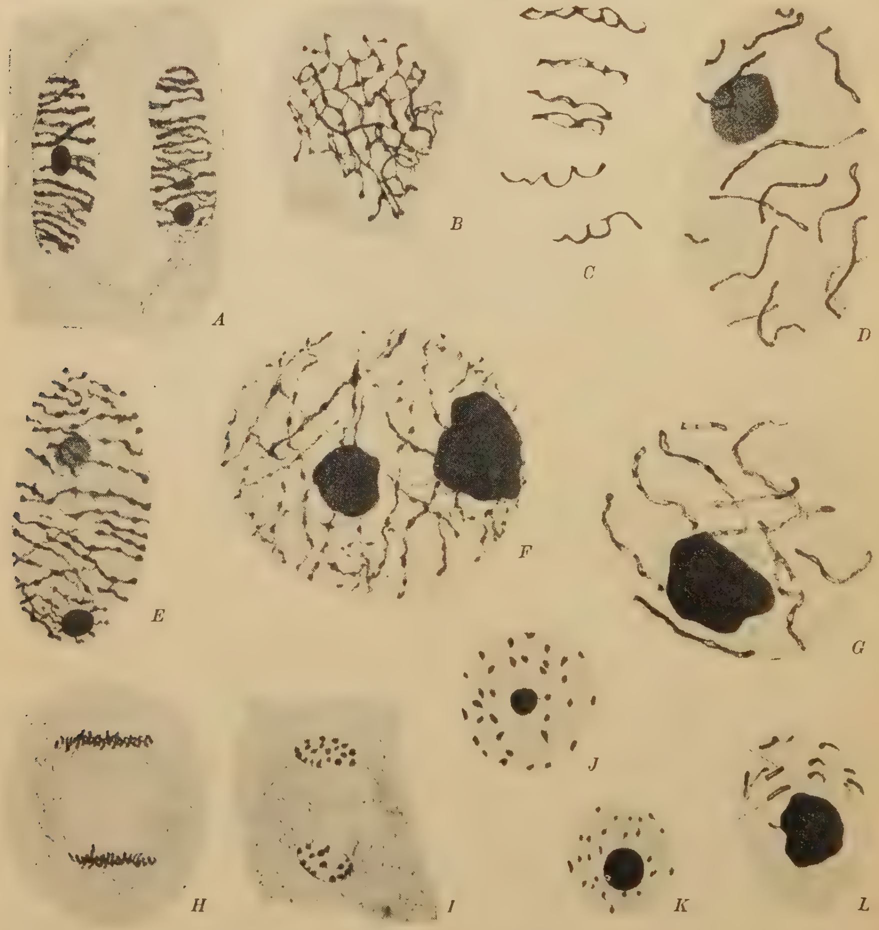

Fig. 54.—Somatic mitosis in plants with small or slender chromosomes. *A–D*, chromosomes of intermediate diameter: *A*, telophase in *Blechnum; B*, interphase in *Blechnum; C*, prophase chromosomes in *Blechnum; D*, prophase in *Marattia*. *E–G*, slender chromosomes: *E*, telophase in *Ceratopteris; F*, interphase in *Pteris; G*, prophase in *Polypodium*. *H–L*, very small chromosomes: anaphase, telophase, interphase, early prophase, and late prophase in *Azolla*. (*After de Litardière*, 1921*b*.)

than anastomosis during the telophase, and remain clearly visible through the interphase. In the prophase the anastomoses are retracted, after which the chromosomes elongate slightly, split, and again shorten.

These cases throw some light on several problematic points which were brought up in the foregoing section, and of which two may be mentioned. First, in the case of the very slender chromosomes, there is no ground for the view that splitting is accomplished through telophasic alveolation, for alveoles do not occur. De Litardière finds splitting to take place in slender prophasic threads in all four modes; alveolation is another process which bears no relation to splitting. Second, it is clear also that in the very slender and small chromosome species the karyolymph cannot originate in alveoles, for there are no alveoles. Here it must either arise at the surface of the chromosomes as a result of some interaction with the cytoplasm, or more probably, as de Litardière believes, it must move in from the spindle region as the chromosomes separate and become anastomosed during the telophase. The relation of this karyolymph to the alveolar substance of larger chromosomes has yet to be elucidated. De Litardière's figures of large and intermediate chromosomes seem to show that the karyolymph is of extra-chromosomal origin, and that the alveolar substance may be added to it. The nuclear membrane he regards as not chromosomal, but cytoplasmic in origin.

**The Nucleolus in Mitosis.**—In Chapter IV attention was called to various views which have been held regarding the significance of the nucleolus, and the probability that this body functions largely through interactions with the karyotin was pointed out. Although the view that it is a by-product (Haecker) is suggested by certain cases (fungi) in which passes bodily into the cytoplasm at the time of mitosis, and although the opinion (Strasburger, Němec) that it is a reserve substance for the achromatic figure is suggested by its frequent disappearance as the figure develops, it is now becoming increasingly apparent that in ordinary cases the significant nucleolar changes are those which are correlated with alterations in the chromosomes.[1]

Among the recent works in which evidence on this point has been submitted may be cited those of de Litardière (1921*b*) on the ferns, Martens (1922) on *Paris quadrifolia*, Van Camp (1924) on *Clivia miniata*, and Cleland (1924) on *Œnothera franciscana sulphurea*. In ferns with small chromosomes de Litardière observes an inverse relation between the chromaticity of the chromosomes and the volume of the nucleolar mass. He interprets this to mean that chromatic matter passes out of the chromosomes in the telophase and forms the nucleolus, which is largely transferred to the chromosomes again late in the ensuing prophase. Just such an apparent transfer of chromatic matter was described by Strasburger (1907) and Berghs (1909) in *Marsilia*. In *Paris* Martens finds that an achromatic matrix of the chromosome assumes a decided chromaticity during the late prophase, metaphase, and anaphase, and loses it again in the telophase (Fig. 58). This he believes is probably due to a transfer of the chromatic nucleolar substance to the matrix during these stages, since the nucleolus disappears as the chromaticity of the matrix develops, and reappears as it is lost. Van Camp has made a special study of this question, using the root meristem of *Clivia* (Fig. 55). The reticulm is basophile, whereas the nucleolus consists of a substance which is acidophile and iron-avid; and the two are in direct contact. The developing prophasic spiremes become increasingly iron-avid as the nucleolus decreases in volume, breaks up into fragments, and becomes less iron-avid. By the end of the prophase the nucleolar material has usually passed entirely to the chromosomes; in case any remains it is resorbed in the cytoplasm. The nucleolar substance is not thought simply to impregnate the chromosome, but the two form a special complex ("kinochromatin"). In the telophase the two substances are again dissociated: the iron-avid and acidophile substance appears at certain points along the chromosomes in the form of small globules, which then fuse to form the new nucleoli. Similar evidence for the transfer of a chromatic material from the nucleolus to the developing spiremes by way of one or two prominent strands is found by Cleland in the microsporocytes of *Œnothera*. Here the nucleolus remains as a pale body after the chromatic matter has left it. Many observers have reported that the nucleolus stains deeply during the early prophase and more faintly in the late prophase of the first meiotic division.

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[1] For authors holding this general opinion, see footnote on p. 9.

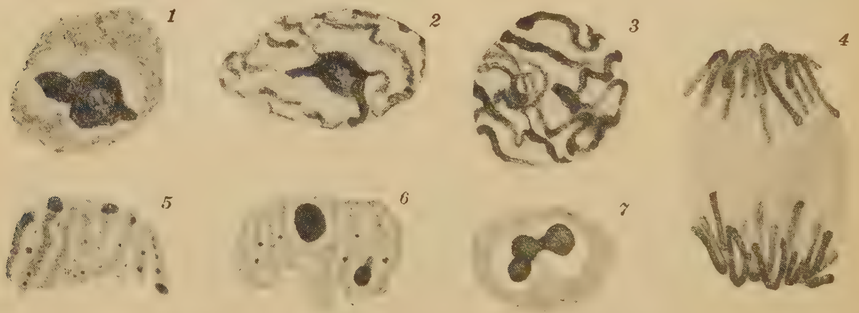

Fig. 55.—The behavior of the nucleolus during somatic mitosis in *Clivia miniata*. 1–3, prophase; 4, anaphase; 5–7, telophase. (*After Van Camp*, 1924.)

More extreme examples of this type of nucleolar behavior have been known for many years in certain green algæ, notably *Spirogyra*. Here practically all of the chromatic substance is confined to a large nucleolus, the reticulum being extremely delicate. It was the opinion of Berghs (1906), Karsten (1908), and Tröndle (1912) that all of the chromosomes are developed from this nucleolus in the prophase. Strasburgher (1888) had stated that they arise from the reticulum. Van Wisselingh (1898, 1900, 1921) has held that there are chromosomes of two kinds in *Spiro-*

*gyra*, two of them arising at least in part from the nucleolus and the others wholly from the reticulum. In *Zygnema* both Escoyez (1907*a*) and van Wisselingh (1914) found that the reticulum develops all of the chromosomes, though chromatic matter is transferred from the nucleolus. Similarly, in *Mougeotia* (Peterschilka, 1922) and *Cladophora* (T'Serclaes, 1922), the chromosomes are all of reticular origin. These seem to represent conditions intermediate between ordinary nuclei and the "karyosome nuclei" of certain Protista, which show various degrees of union of chromosomal, nucleolar, and other substances to form a permanent and regularly dividing *karyosome* (Chapter XII).

These examples suffice to show that there is a significant relationship between the nucleolar substance and the cyclic alterations of the chromosomes, but the nature of this relationship has yet to be determined.

**The Structure and Division of Chromosomes.**—The fundamentally important questions of the minute structure of the chromosome and the mode of its division may now be examined more closely. Many controverted points are here involved, and a final evaluation of the many opinions is at present impossible, but they must be set forth if one is have a proper conception of this important subject. The chief questions at issue center around the origin of the slender filament which appears in the early prophase, and the manner in which it becomes longitudinally double somewhat later. It is natural that large chromosomes should have been chosen for the investigation of these points, and it is consequently with them that the following discussion will chiefly deal.

*Origin of the Prophasic Thread.*—According to the main interpretation of chromosome structure set forth in the foregoing pages, the form of a slender thread is first assumed in the prophase. The karyotin making up the resting interphase reticulum gradually collects along the more prominent strands of the reticulum until each chromosome is represented by a single contorted filament. The reticulum itself arises through a process of "alveolation" in the preceding telophase. The exact details of this telophasic transformation are in doubt, but in the chromosome one observes the appearance of achromatic areas, or "alveoles," which enlarge and coalesce to form a more or less continuous achromatic matrix with a problematic relation to the karyolymph. This process involves the assumption of a reticular form by the chromatic karyotin. In certain very large chromosomes the alveolar condition is observable as early as the metaphase, and it seems not unlikely that in such cases the chromosome throughout most of the nuclear cycle may be in the alveolar condition, this becoming more distinctly visible in the telophase because of alterations in the chromaticity of the "achromatic" substance constituting the alveoles. The main point is that the karyotin, although it may often appear in the form of a contorted thread in certain chromosomes owing to the arrangement of the alveoles, does not assume the form of a single continuous filament until the prophase; the filament is a more or less temporary stage in the chromosome cycle.

Contrasted with the above interpretation is that made by the advocates of the *chromonema hypothesis.* That the chromatic substance frequently appears as a contorted or spiral filament in the telophase as well as the prophase was reported by a number of early observers; in fact, Baranetzky described spirals in *Tradescantia* as long ago as 1880. Janssens (1901) suggested that the telophase spirals are the same as those observed by himself and many others in the prophase. This conception was embodied in the chromonema hypothesis, developed especially by Bonnevie (1908, 1911) and Vejdovský (1912). As a result of her studies on *Ascaris, Allium,* and other forms Bonnevie concluded that each chromosome in the telophase differentiates an endogenous spiral thread which persists through the interphase and emerges from the chromosome in the following prophase as the slender filament, which is later split (Fig. 56, *B*). The achromatic material is not continuous from one nuclear generation to the next, but is differentiated anew in each telophase as the spiral develops. According to Vejdovský, who first applied the term "chromonema" to the spiral filament, the latter arises much earlier than stated by Bonnevie; it first develops in the prophase within the yet unsplit antecedent chromonema, and as the latter splits the new chromonema becomes broken up into irregular rings or strands, which in some undetermined manner form a continuous spiral again in the telophase. The achromatic portion of the chromosome swells and becomes the karyolymph, at whose periphery the nuclear membrane is formed. These investigators have therefore regarded the chromatic filament, or chromonema, as a structure present throughout most or all of the nuclear cycle, rather than a temporary condition related to prophasic splitting.

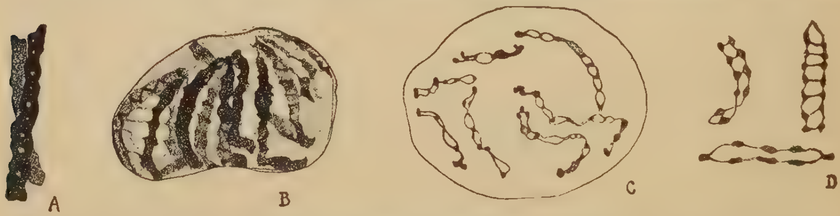

FIG. 56.—*A*, vacuoles in chromosomes at metaphase in *Trillium.* (*After Grégoire and Wygaerts,* 1903.) *B*, spiral arrangement of chromatic material within the chromosomes of *Allium.* (*After Bonnevie,* 1911.) *C, D*, stages of chromosome splitting in *Najas marina,* showing chromomeres. (*After Müller,* 1912.)

A further development of the chromonema hypothesis is found in the view of those who report a doubling of the chromonema during the anaphase or even earlier, the chromatic material of each chromosome existing through the anaphase, interphase, and prophase as a pair of intertwined spirals.[1] The most recent work of this nature is that of Kaufmann on *Tradescantia pilosa* (Fig. 57).[2] During the metaphase and anaphase this investigator observes two such spiral chromonemata coiled within the achromatic matrix of each daughter chromosome. In the telophase the substance of the matrix becomes continuous with the karyolymph, leaving the pair of spirals to maintain the genetic continuity of the chromosome through the ensuing interphase. In the prophase, as the two spirals shorten and thicken, chromomeres appear in them, and seem to represent centers at which a new differentiation of achromatic

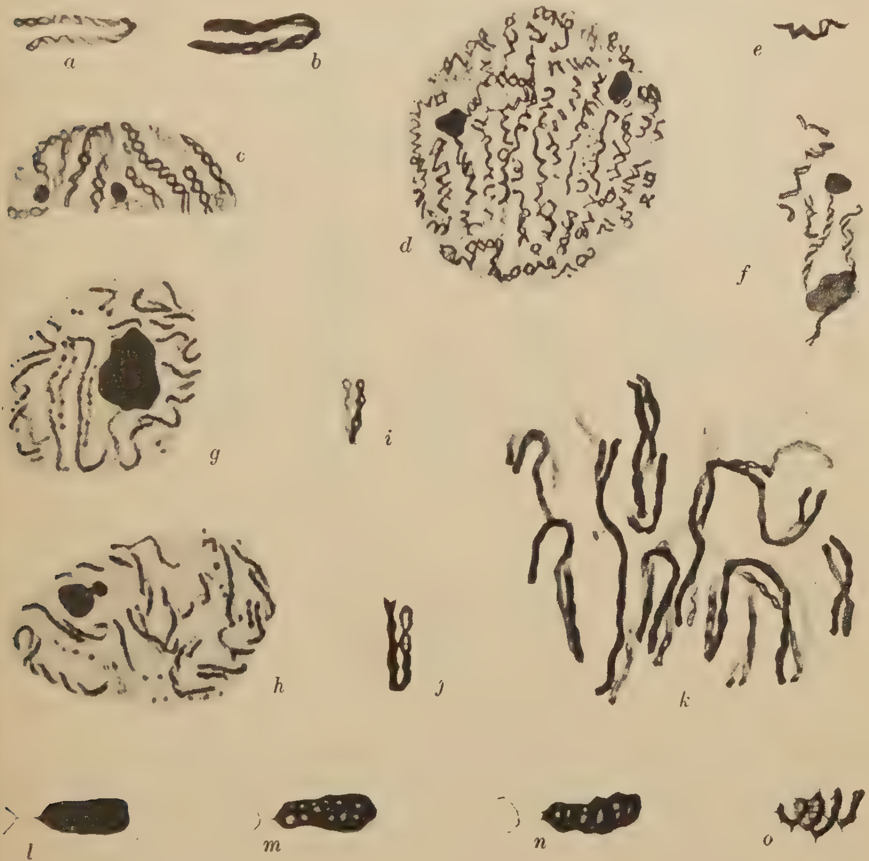

Fig. 57.—Mitosis in *Tradescantia pilosa*. *a*, *b*, anaphase. *c*, telophase. *d*, *e*, interphase. *f–h*, prophase. *i*, *j*, appearance of split. *k*, metaphase. *l–o*, chromosomes in the prophase of the first meiotic mitosis, showing aspects observed after different fixations. (*After Kaufmann*, 1926.)

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[1] Dehorne (1911) on *Salamandra* and *Allium;* K. Schneider (1910) on *Salamandra;* Brunelli (1911) on *Tryxalis;* Kaufmann (1925, 1926) on *Tradescantia pilosa.*

[2] The author is much indebted to Mr. Kaufmann for this figure and for permitting the reading of his manuscript in advance of its publication.

substance is beginning. Furthermore, each of the spirals is thought to develop a longitudinal split during the late prophase, so that in the metaphase what ordinarily appears as a double chromosome really has a tetrad structure, since each half contains a pair of spirals. Hence, it is in the prophase that the true splitting of the chromosome is initiated, but separation along this split is not to occur until the second succeeding anaphase.

A different interpretation of the chromatic filament has recently been given by Martens (1922, 1924, 1925) for *Paris quadrifolia* and *Listera ovata.* The chromosome throughout the cycle, according to Martens, is composed of two morphologically distinct constituents: a homogeneous achromatic matrix distinct from the karyolymph, and an imbedded "chromonematic element" (Fig. 58). In the early prophase the chromonematic element has the form of transverse or oblique curved strands lying peripherally in the matrix; many of these are joined to form a zigzag thread, but they do not constitute a continuous spiral throughout the length of the chromosome. Later in the prophase they do become continuous; and after the division of the chromosome (which does not involve an actual splitting of the chromatic filament, as will later be shown) the chromonematic element, at all times accompanied by its achromatic matrix, retains the form of a continuous zigzag thread until late in the interphase, when it becomes broken up into irregular strands. According to this interpretation, therefore, the chromonema is a constant structural element of the chromosome. Martens differs decidedly from

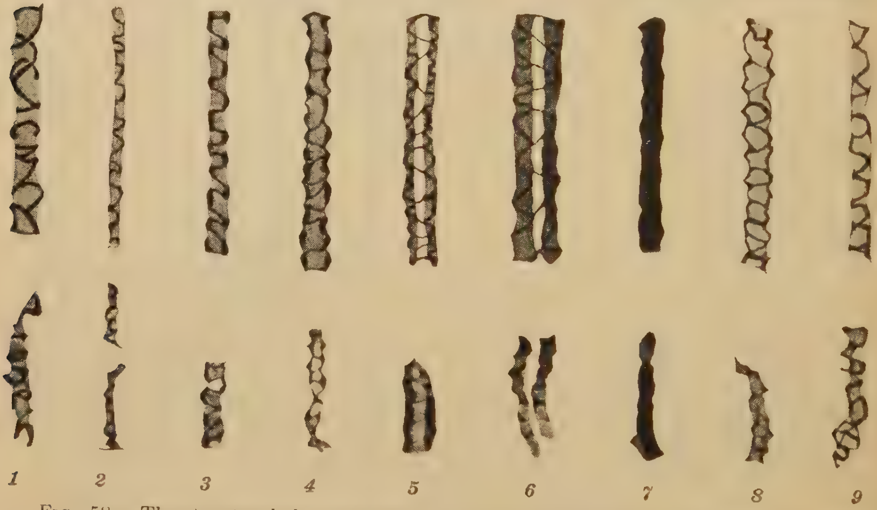

FIG. 58.—The structural changes undergone by the chromosome in the somatic nuclear cycle in *Paris quadrifolia*. Drawings of portions of the chromosomes are shown in the lower row, and diagrams of the corresponding stages above them. 1, 2, early prophase; 3, 4, bilateral repartition; 5, division of achromatic chromosomal matrix; 6, end of prophase, and metaphase; 7, anaphase; 8, telophase; 9, interphase. (*After Martens*, 1922.)

Bonnevie and Vejdovský, however, in maintaining that this element is not always in the form of a continuous thread, that it is accompanied throughout the cycle by its own achromatic matrix, and that it does not actually split. Martens finds further that during the late prophase, metaphase, and anaphase the matrix shows a pronounced chromaticity, which seems to be related to nucleolar activity. As a result, the structure of the chromosome is obscured during these stages and reappears in the late anaphase and telophase.[1] Support for this view of chromosome structure is found by de Litardière (1925) in certain phenomena observed in roots subjected to the action of heat.

Lee (1924) describes the chromosome of *Paris quadrifolia* as a body having at certain stages a distinct spiral chromonema in a less chromatic cylinder, but he adds that it also possesses a rather thick achromatic sheath, with the periphery of which the chromatic spiral is connected by a spiral flange. Other observers (de Litardière, 1921*b*) do not agree that the sheath is actually a part of the chromosome.

A further general view of chromosome structure is that the achromatic matrix encloses a number of discrete chromatic units, or *chromomeres*, which may in turn be aggregates of still smaller granules. In the prophasic thread these unite in one or more regular rows in the matrix, which is also a constant element. This interpretation is widely represented in the literature (see p. 166), and it has recently been emphasized anew by Sands (1923) as a result of his studies on the chromosomes of *Tradescantia* treated by the acetocarmine process (Fig. 59).

Finally, it may be noted that many observers, including those upholding the above interpretations, have described the metaphase or anaphase chromosome as having fairly distinct axial and peripheral portions differing in chromaticity. Chambers (1915) and Chambers and Sands (1923) find that living chromosomes may show an optical difference in these two regions.

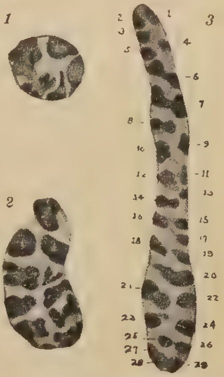

Fig. 59.—The structure of the chromosome in the meiotic phase of *Tradescantia* after treatment with acetocarmine. (*After Sands*, 1923.)

The problem at present confronting students of chromosome structure is to place the proper evaluation upon these appearances presented by chromosomes under the microscope. It seems clear that the chromatic substance which has been called karyotin, and which is arranged in a slender thread with or without achromatic elements in the prophase, is a constant nuclear constituent. It has been variously described as having the form of granules, irregular short strands, a continuous spiral chromonema, a spongy framework, and a cortical sheath. All of these aspects have been observed in sectioned material fixed by the older methods, as well as in whole chromosomes prepared by the recently readopted acetocarmine process. Opinions differ widely with respect to which are natural aspects and which are artifacts. Probabilities seem to favor the naturalness of a regular type of structure, such as is exemplified by chromonemata, as against the irregularity characterizing a spongy framework arising through alveolation, or a matrix with scattered granules. Unfortunately, researches on living material have not progressed far enough to warrant any answer to this important question. Doubtless all the appearances are in some degree unnatural; the actual structure of an untreated chromosome will be exceedingly difficult to disclose. In this connection the need for thorough investigations on the action of various agencies on protoplasmic colloids cannot be too strongly emphasized.

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[1] In the chromosomes of *Trillium grandiflorum* the present author observes a chromonema structure during prophase, metaphase, and anaphase. The appearances are in many points strikingly similar to those figured by Martens, but it is too early to state in what measure the interpretations of that investigator will be found applicable to *Trillium*.

*The Division of the Chromosome.*—It may now be inquired by what method the chromosomal thread, whatever its relation to structures present at other stages, becomes longitudinally double during the prophase. Many years ago Roux (1883) asserted that the complicated process of mitosis is meaningless unless the chromatic matter is qualitatively unlike in different regions of the nucleus, the arrangement of this matter in the form of a long thread prior to its splitting being a means whereby all the qualities, arranged in a linear series in the thread, are equationally divided and distributed to the daughter nuclei. This hypothesis, which involves the conception of the nucleus as an organ of heredity, was founded in part on the theory of Balbiani (1876) and Pfitzner (1881) that the small chromatic lumps (*chromomeres:* Fol, 1891) visible in the nuclear reticulum arrange themselves in a series in the chromosomal thread of the prophase, and by their division initiate its splitting. The view that the chromomeres are of more fundamental importance than the chromosomes in which they lie, and bear some relation to the qualities of Roux, has been widely adopted by cytologists. It has further been supposed that the chromomeres are aggregates of still smaller units—the oxychromatin and basichromatin granules of Heidenhain (1894), which Eisen (1899) termed *chromioles;* and that these chromatic elements are supported in an achromatic substance (*linin*) which makes up the reticular framework of the nucleus.

Occasion has already been taken to point out the present tendency to look upon the reticulum as a single substance (karyotin) whose staining reactions vary under certain conditions, rather than a combination of two distinct substances (chromatin and linin) (see p. 88). Accordingly, the chromomeres are interpreted as thick regions in the karyotin thread rather than chromatin units supported by another material. The question of the autonomy of these chromomeres has long been debated, probably because they appear with such different degrees of distinctness in different organisms. They are well differentiated in animals, particularly in insects. For example, in the grasshopper, *Phrynotettix magnus*, Wenrich (1916) has shown that they are relatively constant in size and position in a given member of the chromosome complement, even in different individuals (Fig. 65). A similar situation has been found in *Dendrocœlum lacteum*, a triclad worm, by Gelei (1921). Many instances might be added in which the chromomeres show a remarkably regular arrangement and division during mitosis.

In other organisms, especially among plants, the karyotin lumps do not show such indications of autonomy. A number of botanists[1] have described regularly behaving chromomeres, especially in microsporocytes of flowering plants. In most of the recent works[2] on somatic mitosis, however, there has been found very little evidence of such regular behavior. Many have, therefore, opposed the view that the chromomeres are significant autonomous units, and have suggested other explanations for the appearances observed. According to a modification of the chromomere theory adopted by Müller (1912) the portions of the thread between the chromomeres split first, the division of the chromomeres following (Fig. 56, *C*, *D*). Müller's figures, which are very similar to those of Strasburger (1907*b*), may be interpreted as stages in the division of a thread without distinct chromomere units. At a certain stage in *Vicia*, for example (Figs. 52 and 53, *S*) the incompletely split chromosome has the form of two parallel strands connected by heavy cross-pieces. The material constituting the cross-pieces gradually moves to the two side strands, the center portion of the cross-piece becoming progressively thinner, and the material accumulating on the side strands as a pair of chromatic lumps. Although some of the cross-pieces may persist until a relatively late stage, most of them soon disappear completely, and the material in the two chromatic lumps is gradually distributed more or less evenly along the parallel strands, which represent the daughter chromosomes resulting from the split. Reference has been made to Kaufmann's idea that the prophasic chromomeres in *Tradescantia* represent points at which a new differentiation of achromatic chromosomal substance is beginning in the chromatic filaments.

It may be well for the present to harmonize these diverse conditions on the basis of the tentative hypothesis that certain chromosomal materials (possibly small units) vary considerably in their distribution in the chromosome in different organisms, and at different stages in the same organism. In some cases these materials may be rather uniformly distributed, whereas in others they may accumulate in smaller or larger amounts in connection with the functional differentiation of various portions of the chromosomal thread, thus giving rise to the visible structures known as chromomeres. Agar (1923) remarks that chromomeres appearing in fixed material "correspond to real local differentiations of the substance of the chromosome, though the actual shape which they assume (namely, bead-like swellings on a fine thread) may be assumed, or at least exaggerated, under the stress of the fixative." However one views the question of their autonomy, the chromomeres in certain cases, together with other features described in the next chapter, seem clearly to indicate a longitudinal differentiation of the chromosome; and even when no chromomeres are visible the arrangement of the chromosome in the form of a thin thread and its accurate splitting into two similar halves are very suggestive in connection with the theory of Roux.

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[1] Strasburger (1884, 1888), Allen (1905), Mottier (1907), Overton (1911, 1922).

[2] Grégoire and Wygaerts (1903), Martins Mano (1904), Grégoire (1906, 1907), Maréchal (1907), Bonnevie (1908), Stomps (1910), Lundegårdh (1912), Sharp (1913, 1920), Tischler (1908, 1921), de Litardière (1921*b*).

It has not yet been found possible to determine exactly by what means such prophasic threads are split. Settlement of this point is greatly to be desired because of its importance in connection with current theories of the mechanism of heredity, but so far it has been prevented by the tenuity of the structures in question. The open spaces through the thread (Fig. 52, *S*) develop from minute light spots which have been interpreted variously as (1) axial alveoles, which soon break through opposite sides of the thread; (2) depressions or grooves, which develop on opposite sides and meet in the axis to form holes; and (3) regions within the thread, from which the chromatic matter retreats toward the two sides of the thread without the formation of distinct alveoles. By whatever means the holes arise, it is clear that they develop into the complete split through the movement of the material between them to the two sides of the thread, as has already been shown. With one or two exceptions, investigators are agreed that the thread becomes double through an actual splitting.

A unique interpretation of chromosome division not involving a real splitting of the chromatic filament has been made by Martens in his works on *Paris* and *Listera* (1922, 1924, 1925) (Fig. 58). During the prophase the chromosome elongates, the chromonematic element taking the form of a slender filament with the achromatic matrix condensed irregularly about it. As the chromosome again shortens and thickens, the matrix regains its regular lateral outlines and becomes a flattened ribbon. The zigzag chromonematic element now undergoes not a splitting, but a "bilateral repartition:" the chromatic substance flows from its transverse portions and collects at its angles along the margins of the ribbon, thus forming two lateral rows of swellings connected by the remaining attenuated transverse portions. These swellings become somewhat elongated, and as the chromosome shortens further those in each row unite to form a continuous filament along the chromosome margin. The two marginal filaments are thrown into zigzags by the continued shortening of the chromosome. The achromatic ribbon then divides by a simple repartition into two longitudinal portions, completing the division of the chromosome, except for a few fine chromatic connections which remain until the anaphase.

This conception, which is at variance with those of all other workers, will be seen at once to involve a point of the greatest importance with respect to the rôle of the chromosomes in heredity. It has been generally supposed that the chromatic element of the chromosome represents the substance primarily concerned in this function, a conception which has found strong support in the apparently accurate equational splitting of every portion of the chromatic thread in somatic mitosis reported by many cytologists. In the process described by Martens, on the other hand, the chromosome as a whole undergoes a longitudinal division, but some portions of the chromatic thread go only to one daughter chromosome, while the remaining portions go to the other. Proof of the correctness of this interpretation would seem to call for some modification of our notions regarding the position of inheritance units within the chromatic thread. Further investigations on this point are consequently awaited with interest.

**Summary and Conclusions.**—In a somatic nuclear division the reticulum becomes transformed into a number of slender threads during the prophase; these threads represent the chromosomes which together constituted the reticulum. Each chromosome thread undergoes an accurate longitudinal splitting. The resulting double threads shorten and thicken, and take their places in the equatorial plane of the achromatic figure. In the anaphase the halves of each double chromosome (the two daughter chromosomes) separate and pass to opposite poles of the figure. The chromosomes of each polar group become internally transformed and combine during the telophase to form a new nuclear reticulum, in which the limits of the individual chromosomes may or may not become obscured.

Anticipating evidence to be presented in the following chapter, it may further be stated that in any particular kind of organism the chromosomes in the nucleus are definite in number, and are differentiated among themselves in function and frequently in form and structure; they constitute a definitely organized system. Moreover, this organization is maintained by virtue of the genetic continuity of each chromosome through successive nuclear generations. In view of these facts, it appears that the outstanding significant feature of somatic mitosis is this: each chromosome is longitudinally divided into equal halves which are distributed to the two daughter nuclei. These two nuclei are consequently similar to each other and to the mother nucleus as regards their chromosome complements; in other words, *somatic mitosis is equational.* Furthermore, since all the nuclei of the body have normally descended through such mitoses from a single nucleus, each of these nuclei contains descendents of all the chromosomes present in the first nucleus of the series: *the somatic nuclei are all alike in their chromosome complements,* barring, of course, the effects of mutation and occasional aberrant chromosome behavior. The great theoretical importance of these features of somatic nuclear behavior will be apparent when we take up the matter of the application of cytological phenomena to the problems of heredity and development.

# CHAPTER X

## THE INDIVIDUALITY OF THE CHROMOSOMES

In later chapters the question of the significance of the nuclear structures in heredity is to be considered. In connection with this question it is of the highest importance to determine whether or not the chromosomes to which the reticulum gives rise in the prophase of mitosis are in any real sense the same as those which went to make up the reticulum in the preceding telophase. That they do preserve their identity as individuals through the metabolic stage, arise only by division, and therefore maintain a genetic continuity throughout the life cycle, was held by van Beneden (1883), Rabl (1885), and Boveri (1887, 1888*b*, 1891) many years ago, and since that time the idea has received the support of a large number of investigators. In this chapter will be briefly reviewed some of the evidences which have led the majority of cytologists to the view that the chromosomes, "if . . . not actually persistent individuals, as Rabl and Boveri have maintained, . . . must at least be regarded as genetic homologues that are connected by some definite bond of individual continuity from generation to generation of cells" (Wilson, 1909).

**The Frequent Persistence of Visible Chromosome Limits in the Nuclear Reticulum.**—In the foregoing description of the behavior of the chromosomes in mitosis it was pointed out that in rapidly dividing tissue the telophasic transformation of the chromosomes and their anastomosis to form the reticulum often do not proceed far enough during the interphase to obliterate the boundaries between the chromosomes, which separate again in the ensuing prophase without having lost their visible identity. In such nuclei, especially those with small chromosomes, there can be little doubt that the autonomy of the chromosomes is preserved. In other cases, however, the telophasic transformation is more complete and the resulting reticulum reacts very weakly to the stains, so that the limits of the constituent chromosomes disappear from view completely. Many workers have, therefore, objected to the statement that here also the chromosomes are present as individuals, although invisible. Haecker (1902) and Boveri (1904) pointed out that this objection may be met by assuming that it is the achromatic framework of the chromosome, and not a chromatic fluid held within it, that maintains a structural independence.

Special emphasis was laid upon this interpretation by Maréchal (1904, 1907) as a result of his studies on the growth stage of animal oöcytes. At this period in the development of the ovum the chromosomes assume a finely branched form (Fig. 111, stage 10) and their ordinary staining capacity is wholly lost. Although chromatic fluid may flow from the reticulum to the nucleolus and back, and may periodically undergo chemical changes which radically alter its staining reactions, the achromatic chromosomal substratum nevertheless maintains an uninterrupted structural continuity. The chromosome, as Maréchal urges, is not simply a mass of chromatin, but rather "a structure periodically chromatic;" hence the loss of chromaticity does not signify the loss of structural continuity on the part of the chromosome. This view has the support of the earlier observation made by Boveri (1887*a*, 1888*a*, 1891; also 1909) and confirmed by Herla (1893), that the chromosomes in the segmenting egg of *Ascaris* have a certain arrangement when they build up the nuclear reticulum in the telophase, and reappear from the reticulum in the same position in the next prophase.

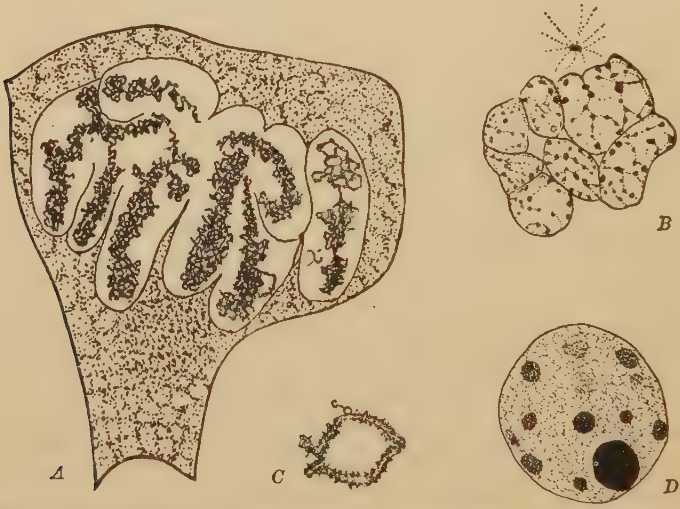

Fig. 60.—Some evidences for chromosome individuality. *A*, chromosomal vesicles in *Brachystola; X*-chromosome in vesicle at right. (*After Sutton*, 1902.) *B*, chromosomal vesicles in *Fundulus* embryo. (*After Richards*, 1917.) *C*, chromomere vesicle (*c*) on chromosome of *Chorthippus*. (*After Wenrich*, 1917.) *D*, prochromosomes in *Pinguicula*.

The independence of the chromosomes is especially evident in the case of "chromosomal vesicles," or "karyomeres," which have frequently been observed in various organisms (Fig. 60, *A*, *B*). In the spermatogonia of *Phrynotettix*, for example, Wenrich (1916) has shown that each of the alveolizing chromosomes forms its own vesicle about it in the telophase, the several vesicles joining to form a common nucleus. In some cases the boundaries between the vesicles do not entirely disappear during the resting stages, and in the next prophase the chromatic material of each vesicle organizes in the form of a chromosome. The same condition is found in the nuclei of *Fundulus* (Richards, 1917), *Crepidula* (Conklin, 1901*a*), and certain fish hybrids (Pinney, 1918). In extreme cases the chromosomes may form what is virtually a group of separate small nuclei. Thus in the blastomeres of *Pediculopsis graminum* Reuter (1909) finds that the four chromosomes organize distinct nuclei, which form four parallel spindles at the time of division ("merokinesis").

**Persistence of Parental Chromosome Groups after Syngamy.**—In Chapter XV it will be shown that in syngamy there are brought together two sets of chromosomes, one set from each parent; and that in every nucleus of the resulting individual the chromosomes furnished by the two parents are present together, all of them dividing at every mitosis. When the chromosomes of the male parent are similar to those of the female parent it is usually impossible to distinguish them in the nuclei of the offspring. In a number of cases, however (Fig. 160, *B*), the two parental groups are distinguishable in the mitotic spindle, and often at other stages, through several embryonal cell generations.[1] It is in hybrids that this phenomenon is shown most strikingly. In hybrid fishes obtained by crossing *Fundulus* with *Menidia* Moenkhaus (1904) was able to distinguish easily between the long (2.18$\mu$) chromosomes of *Fundulus* and the short (1$\mu$) ones of *Menidia*. Here, as in *Crepidula* and *Cyclops*, the paternal and maternal chromosomes form separate groups in the mitotic figure. A similar condition was seen by Tennent (1912) in hybrid echinoderms obtained by crossing in various ways *Moira*, *Toxopneustes*, and *Arbacia*. In the later cell-divisions the parental chromosomes mingle more or less, but are nevertheless distinguishable. In *Fundulus-Ctenolabrus* hybrids (Morris, 1914; Richards, 1916), as well as in the normally fertilized *Cryptobranchus* (Smith, 1919), the chromatic contributions of the two parents are distinguishable even in the metabolic stage of the nucleus. Among both plants and animals there are now known many cases in which the chromosomes of the two parents, even though they do not remain in distinct groups, may easily be distinguished in the hybrid. Such cases will be considered in Chapter XVII.

**Size and Form of Chromosomes.**[2]—One of the most striking lines of evidence favoring the theory of chromosome autonomy has been found in those plants and animals which show constant differences in size and shape among the various members of each parental chromosome group, so that particular chromosomes are recognizable in the group appearing at each mitosis. Since each parent furnishes a set of chromosomes to the new individual, each kind of chromosome is present in duplicate in the nuclei of this individual. It is therefore customary to speak of the chromosomes as being present in *homologous pairs*, though at most stages of the life history there is ordinarily no actual spatial pairing.

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[1] *Crepidula* (Conklin, 1897, 1901), *Cyclops* (Haecker, 1895*c;* Rückert, 1895), and *Cryptobranchus* (B. G. Smith, 1919).

[2] See the review of this subject by Tischler (1921–1922, pp. 620ff.).

Since the description of the chromosomes of *Brachystola* by Sutton in 1902 (Fig. 61) the reported cases in which the different pairs of the chromosome complement possess different characteristic sizes and shapes have become increasingly numerous. This is notably true of insect cytology.[1] In the sea urchin, *Echinus*, Baltzer (1909) found that the 36 chromosomes have constant differences in length and shape, some being hooked and some horseshoe-shaped. In the flatworm, *Gyrodactylus* (Gille, 1914), there are six pairs, all different in length. In *Ambystoma tigrinum* Parmenter (1919) finds 14 pairs of graded sizes. The researches of Carothers (1921) on *Circotettix*, an orthopteran in which the two members of certain homologous pairs differ in shape, have shown that the chromosome exhibiting the same characteristics in successive generations is actually the same individual (p. 373).

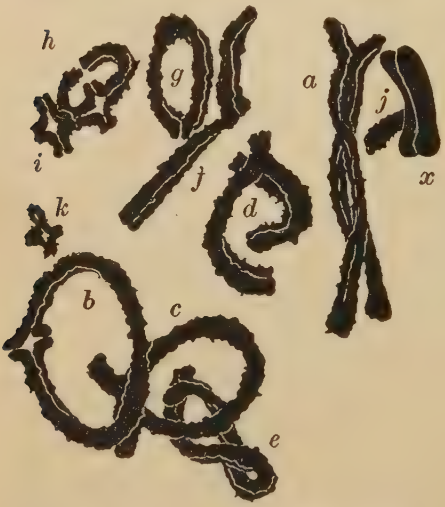

FIG. 61.—The chromosome complement in the spermatocyte of *Brachystola magna*. (*After Sutton*, 1902.)

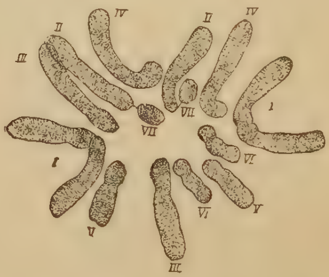

FIG. 62.—The chromosome complement in a somatic cell of *Najas major*, showing the homologous pairs. (*After Tschernoyarow*, 1914.)

Several examples among plants may also be cited. In *Crepis virens* there are three pairs differing markedly in size (Figs. 64, *B*; 180).[2] In *Vicia faba* there are five short pairs and one long pair (Sharp, 1914; Sakamura, 1915) (Fig. 63). *Najas major* has several distinguishable pairs (Tschernoyarow, 1914) (Fig. 62); here the smallest pair is attached to one of the larger pairs, and it now seems probable that these together are really a single pair with pronounced constrictions. In *Galtonia* there are four long, two intermediate, and 2 short pairs (Newton, 1924). In *Butomus*

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[1] See the extensive researches of McClung (1905, 1914, 1917), Robertson (1916), Harman (1915), Carothers (1917, 1921), and others.

[2] Rosenberg (1909*a*, 1918, 1920), de Smet (1914), M. Nawaschin (1915, 1925), W. R. Taylor (1925*c*), Collins and Mann (1923), Mann (1925).

*umbellatus* the 20 pairs of chromosomes fall into six size groups (Terby, 1922). Six classes may also be distinguished among the eight pairs in *Cyrtanthus parviflorus* (W. R. Taylor, 1925*a*) (Fig. 64, *C*).

Not only may certain chromosomes be distinguished on the basis of comparative length, but in some cases there may be other characteristics which serve as marks of identification. In the chromosomes of many plants and animals there are pronounced constrictions in some of the members of the group. It has been shown in a number of instances that these constrictions have constant positions in the chromosome. In *Vicia faba*, for example, Sakamura (1915, 1920) finds that each of the two long chromosomes ("M-chromosomes") of the somatic group has two constant constrictions, one at the middle and one near the end ("m-constriction" and "e-constriction") (Fig. 63, *A*). The m-constriction marks the point of attachment of the spindle fibers. There are also end-constrictions in eight of the ten short chromosomes. Regularly situated constrictions have also been demonstrated in *Fritillaria tenella*

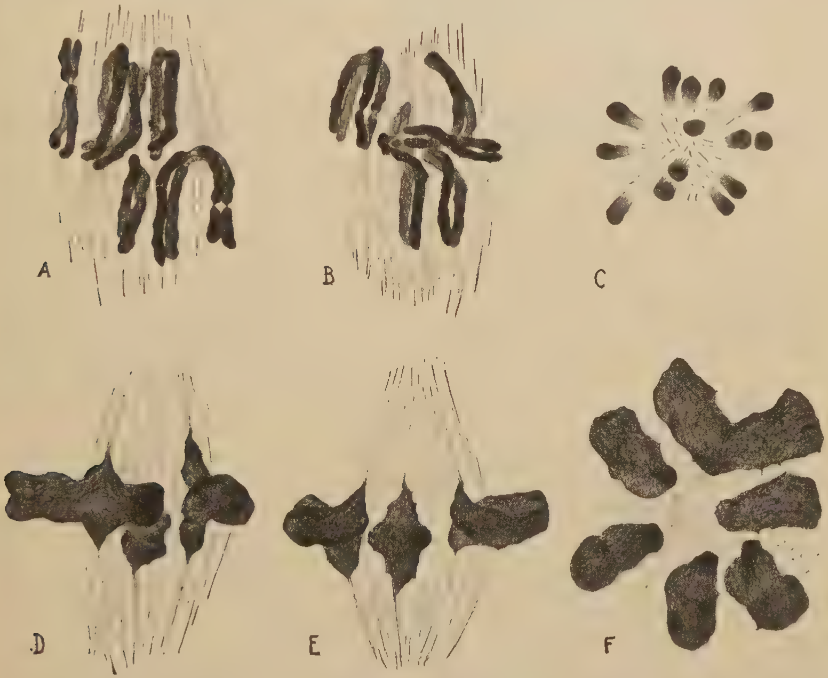

Fig. 63.—The chromosome complement of *Vicia faba*. *A*, *B*, two successive sections of a mitotic figure in the root tip, showing the 12 split chromosomes, 2 of them about twice as long as the other 10. *C*, transverse section of the chromosome group at anaphase: each of the long chromosomes, having a median fiber attachment, passes polewards in the form of a V so that both ends appear in the section; this makes the number apparently 14. *D*, *E*, two successive sections of the first meiotic mitosis in the microsporocyte, showing the 6 bivalent chromosomes: the large one is at the left. *F*, polar view of first meiotic mitosis at metaphase, showing the 6 bivalents.

by S. Nawaschin (1914). Here they are present at the middle of the largest chromosomes, nearer one end in the medium-sized chromosomes, and close to the end in the smallest ones. In *Crepis virens* (M. Nawaschin, 1915) there are constrictions near one end in two of the three chromosomes of the haploid group in the pollen grain, in four of the six chromosomes of the diploid group in the somatic cells, and in six of the nine chromosomes of the triploid group in the endosperm cells. W. R. Taylor (1924) finds that all of the chromosomes in *Gasteria verrucosa* have constrictions: in the four large chromosomes these are near one end in three and somewhat farther back in one; in the three small chromosomes they are also near the end, and two at least of these chromosomes have a second less pronounced constriction near the middle. Taylor (1925) also reports definitely localized constrictions in *Velthemia*, *Allium*, *Cyrtanthus*, *Aloë*, *Haworthia*, and other genera (Fig. 64). Small terminal portions marked off from the rest of the chromosome by distinct constrictions are frequently referred to as "satellites." The elongation of the constrictions at certain stages, notably in the anaphase, gives such chromosomes a very striking appearance. This general condition has also been shown in animal chromosomes, as, for example, in the fish, *Lepidosiren* (Agar,

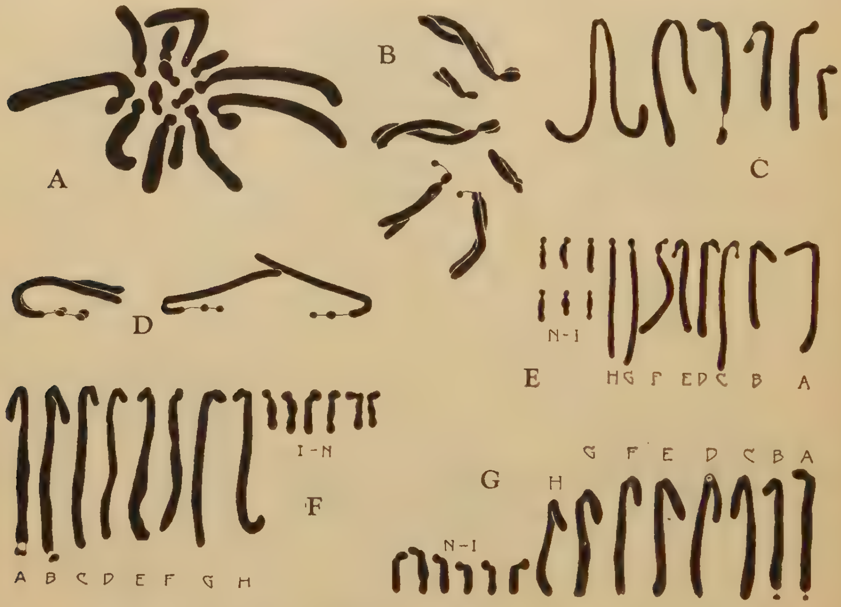

FIG. 64.—The morphology of the somatic chromosomes of several angiosperms. *A*, *Gasteria verrucosa*. *B*, *Crepis capillaris* (*virens*). *C*, *Cyrtanthus parviflorus:* the 6 forms exhibited by the 8 pairs of chromosomes. *D*, *Allium cepa:* chromosomes in metaphase and anaphase, showing two satellites in tandem, an unusual condition. *E*, *F*, *G*, the chromosome complements of *Haworthia cymbiformis*, *Gasteria verrucosa*, and *Aloë arborescens*. (*After W. R. Taylor*, 1924, 1925*ab*.)

1912), and in many insects. On the basis of the widespread occurrence of these definitely localized constrictions it has been possible to interpret a number of hitherto puzzling phenomena, such as certain variations in chromosome number (see below) and various features of the meiotic process.

Other individual peculiarities distinguishing the various chromosomes of the complement are known, especially in the insects. In *Phrynotettix* (Wenrich, 1916) the chromatic lumps, or chromomeres, differ in size and position in the various chromosomes, but show a striking constancy of arrangement in a given member of the complement in different cells and individuals (Fig. 65). Three of the chromosome pairs also differ markedly from the others in stainability and other particulars. Especially noteworthy is the "sex-chromosome" which has been identified in many animals and a number of plants (Chapter XIX). In *Chorthippus curtipennis*, an orthopteran, Wenrich (1917) finds that small "chromomere vesicles" regularly appear at definite points on certain chromosomes (Fig. 60, *C*). Janssens (1924) has described a "proximal granule" attached to one end of each chromosome of *Stethophyma grossum* (Fig. 126, *G*); these granules mark the points at which the spindle fibers are attached. The relative constancy in the location of the point of the fiber attachment for each member of the chromosome complement is one of the most interesting of the evidences for chromosome individuality. It has been shown to hold true in a considerable number of cases, particularly among insects, and is probably the prevailing condition. The location of the fibers is not a matter of chance, but is determined by differentiations of some kind at certain points in the chromosomes. Since these points, which are frequently marked by constrictions or granules, are the first to move toward the poles, their locations are largely responsible for the characteristic shapes assumed by the chromosomes in the metaphase and the anaphase.

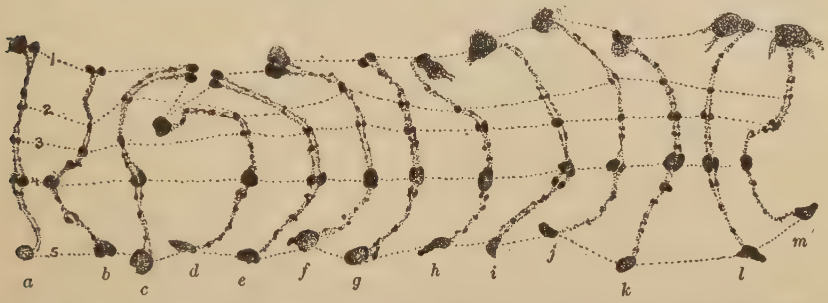

Fig. 65.—Conjugated chromosome pair "B" from the spermatocytes of 13 different individuals of *Phrynotettix magnus*, showing constancy in size and arrangement of principal chromomeres. The same constancy is shown in the different cells of a single individual. (*After Wenrich*, 1916.)

It therefore appears that the chromosomes of a given complement not only maintain a genetic *continuity* through successive nuclear generations, but are also qualitatively different from one another. The fact of their functional differentiation was brought out in certain experiments of Boveri, and has since been more clearly revealed in a variety of cytological and genetical phenomena. Because of their individual peculiarities they are said to have a *specificity*, as well as an individuality, or continuity. Hence they might be likened to a set of unlike tools, or to the series of unlike wheels in a watch. Furthermore, the relatively constant and characteristic positions of constrictions, chromomeres, chromomere vesicles, and proximal granules afford visible evidence that the chromosome is a compound body with some kind of longitudinal differentiation, a conception which is of the highest importance in connection with current views of the rôle of the chromosomes in heredity.

**Prochromosomes.**—Bodies known as prochromosomes have frequently been cited as evidence for chromosome continuity. These small chromatic masses have been described in the nuclei of many plants,[1] and in a few animals. They have been looked upon as portions of chromosomes which have not undergone complete telophasic transformation, and hence as persistent centers about which the chromosomal material condenses in the ensuing prophase. This interpretation may be valid in some cases, particularly those in which the number of prochromosomes in the nucleus seems to correspond to the chromosome number, but in others the significance of such chromatic masses is very doubtful. Often they seem clearly to be new accumulations of karyotin (chromocenters) rather than untransformed portions of the chromosomes; in such cases they have no particular significance for chromosome individuality.[2]

**Chromosome Number.**—It was long ago noticed by Boveri, van Beneden, and Strasburger that the number of chromosomes in any given species is relatively constant.[3] It was largely upon this fact that the theory of chromosome individuality was originally based. The fact that the number of chromosomes appearing at every mitosis is almost invariably the same was taken to mean that the structural indentity of the chromosomes is never lost. Certain observers (Tellyesniczky, Fick,

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[1] In *Thalictrum*, *Calycanthus*, *Campanula*, *Helleborus*, *Podophyllum*, and *Richardia* by Overton (1905, 1909); in the Cruciferæ by Laibach (1907); in *Drosera* and other forms by Rosenberg (1909*c*); in *Acer platanoides* by Darling (1914); in *Musa* by Tischler (1910); and in a number of other forms.

[2] Tischler (1906, 1910, 1921–1922), Grégoire (1907), Gates (1908), Lundegårdh (1910, 1912), Gates and Rees (1921), Mottier (1907), Digby (1914), de Smet (1914).

[3] For lists of chromosome numbers in plants, see Ishikawa (1916), Marchal (1920), and Tischler (1916, 1921–1922). The known numbers in ferns are listed by de Litardière (1921*b*). For the numbers in animals, see Harvey (1916, 1920). Wilson (1925) gives a fairly extensive list for both plants and animals. Winge (1917) discusses at length the general significance of chromosome number; see also Ernst (1922).

Hovasse, Champy) have held that the apparent constancy in number is not due to a structural continuity or individuality of any sort, but rather to the fact that the successive nuclei have a relatively uniform amount of nuclear material, the chromosomes "crystallizing out" of this material in each prophase and going into solution at the close of mitosis. This idea was especially developed by Della Valle (1909, 1912*ab*), who described the formation of chromosomes by the aggregation of fluid crystals during the prophase. The evidence for this view has been criticized by a number of investigators, who have shown it to be untenable.[1]

It will be of interest to review briefly some of the classic experiments on echinoderm eggs which afforded support to the theory of chromosome individuality. Especially noteworthy are the brilliant researches of Boveri (1895*a*, 1902*a*, 1903*a*, 1904*b*, 1905, 1907, etc.).

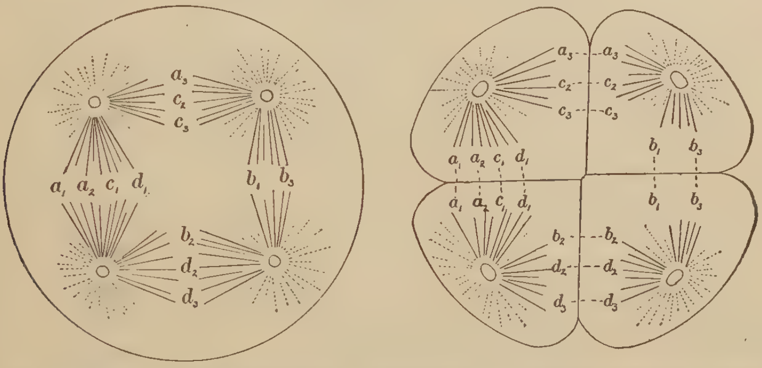

FIG. 66.—Diagram showing the irregular distribution of the chromosomes (indicated by letters) by a quadripolar mitotic figure. (*After Boveri.*)

Boveri found that if the number of chromosomes is increased or decreased by artificial means the altered number appears at every mitosis thereafter. (*a*) An enucleate egg fragment may be entered by a spermatozoön, and may then develop into a larva with half the normal number of chromosomes in every nucleus. (*b*) The unfertilized egg of a sea urchin was caused to undergo division by artificial means, after which a spermatozoön was allowed to enter one of the blastomeres (daughter cells). A larva resulted in which one-half of the cells had regularly 18 chromosomes (half the normal number) while the other half had the normal 36. (*c*) Two spermatozoa occasionally entered one egg; the cells of the resulting larvæ had 54 chromosomes, the triploid number. Abnormal mitotic figures were often formed in such dispermic eggs, bringing about an irregular distribution of the chromosomes. For example, a quadripolar spindle was produced, separating the 54 split chromosomee (108 daughter chromosomes) into four groups, with 18, 22, 32, and 36 chromosomes respectively (Fig. 66). Such abnormal larvæ ("plutei") showed four chromosome numbers in the cells of four different regions of the body. Boveri (1914) later suggested that malignant tumors might be due to such abnormal chromosome distribution. (*d*) The number of chromosomes was doubled by shaking the eggs while the chromosomes were split during the early stages of cell-division. In this manner larvæ were produced with 72 chromosomes, the tetraploid number, in each of their cells. (*e*) In the threadworm, *Ascaris megalocephala*, fertilization of an egg of the variety *bivalens* (two chromosomes) by a spermatozoön of the variety *univalens* (one chromosome) resulted in a larva with three chromosomes in all of its nuclei, the chromosome contributed by the male parent being distinguishable from the other two (Boveri, 1888*a*; Herla, 1893; Zoja, 1895).

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[1] See Montgomery (1910), McClung (1917), Parmenter (1919), and de Litardière (1921*b*).

Results such as the above led Boveri to the conclusion that the number of chromosomes arising from the reticulum in the prophase is directly and exclusively dependent upon the number that went to make it up in the preceding telophase. If a nucleus is reconstructed in the telophase by an abnormal number of chromosomes as the result of a disturbance of the mitotic process, the altered number invariably appears in the succeeding prophase. If extra chromosomes are present they are not eliminated in any way during the resting stages, and if chromosomes have been lost during an abnormal mitosis they are not replaced.

This general conclusion has been strikingly confirmed by more recent researches on the chromosomes of hybrids, by observations on cells subjected to the influence of various agencies causing aberrant chromosome behavior in mitosis, and by critical analyses of the chromosome complements in organisms showing unexplained departures from the normal chromosome number.

It has been found in a large number of instances that the chromosomes of the two parents preserve their peculiar characteristics in the cells of the hybrid, as in Boveri's case of *Ascaris*. Moreover, in such hybrids certain aberrations in chromosome behavior occur at the time of mitosis, giving rise to cells with altered chromosome numbers. The subsequent history of the chromosomes in such cells affords a practical demonstration of their individuality; on no other basis can one so reasonably account for the phenomena observed. These phenomena will be described at some length in Chapter XVII.

That the behavior of the chromosomes can be readily influenced by subjecting tissues to the influence of chloral hydrate and other agencies has been repeatedly shown.[1] In the roots of *Vicia faba*, for example, Sakamura (1920) found that chloral hydrate, benzene vapor, ether, chloroform and the gall-producing secretions of *Heterodera* may be employed to bring about aberrations of the mitotic process. All of them caused the chromosome constrictions to become more pronounced, one or more of the chromosomes thus becoming divided temporarily into several loosely connected smaller parts. Sakamura believes that such accentuation of obscure constrictions and temporary subdivision of the chromosomes will go far toward explaining frequently reported inconstancies in number.

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[1] Němec (1903), Kemp (1910), Strasburger (1911), Sakamura (1920).

McClung (1917) finds in his analysis of the chromosome groups of the orthopterans *Hesperotettix* and *Mermiria* that temporary associations often occur between various members of a group, with the resulting formation of "multiple chromosomes" and a consequent decrease in the apparent number. In *Hesperotettix*, for example, the nuclei normally have 12 pairs of chromosomes, but because of the formation of such multiple chromosomes individuals with apparently 11, 10, or 9 pairs are frequently found (Fig. 67). For a given individual the number so formed is exactly constant, since the members of a multiple remain together through all the mitoses; but for the species it is variable within certain limits, owing to the varying numbers of chromosomes which may become involved in such multiple combinations. In all cases the full number of chromosome pairs is present, but some of them are so combined that there is an apparent, though not actual, variation in the number. A similar condition is found in other forms by Robertson (1916). Of great significance is the further fact that what appear to be occasional associations in *Hesperotettix* are permanent in *Chorthippus*, *Chloeältis*, and *Stenobothrus*, the kind of combinaton and the particular chromosomes

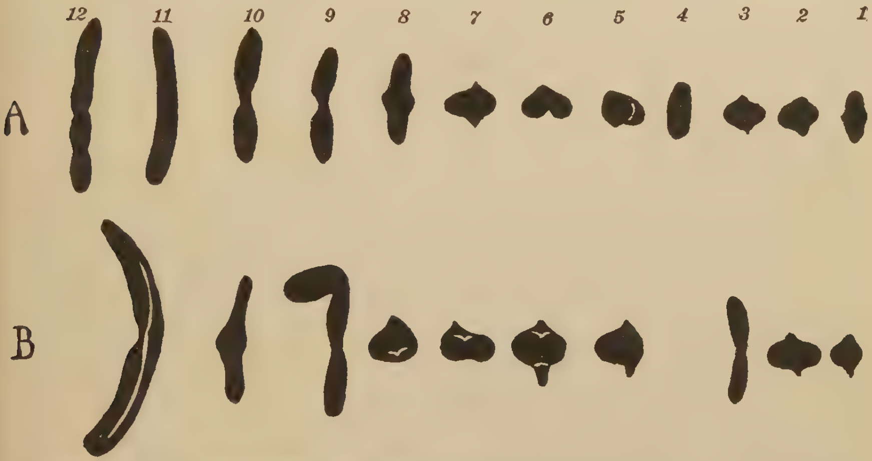

FIG. 67.—The chromosome complement of *Hesperotettix viridis*. *A*, the 12 bivalent chromosomes in the spermatocyte, including the accessory chromosome (No. 4). *B*, complement from another individual, showing two "multiple chromosomes:" Nos. 11 and 12 have united temporarily, as have also Nos. 4 and 9. (*After McClung*, 1917.)

involved apparently being the same in the various genera. This indicates a close relationship not only between the chromosomes of the different nuclei or individuals of a species, but also between those of different species and genera. The union of the two $X$-chromosomes in a strain of *Drosophila,* with interesting effects on the breeding behavior, has been described by L. V. Morgan (1922). A remarkable tendency on the part of somatic chromosomes to form compound chromosomes in the germ cells is described by Walton (1924) for certain parasitic nematodes. In *Ascaris megalocephala* each large autosome in the germ cell may be equivalent to more than 20 somatic elements, while each $X$-chromosome represents 8.

The opposite condition, *i.e.,* the temporary subdivision of chromosomes into smaller units, is also known. In the mosquito, *Culex pipiens,* for example, there are three pairs of homologous chromosomes in the somatic nuclei. During a certain stage in the insect's metamorphosis it has been pointed out by Holt (1917) that the chromosomes may split repeatedly, giving nuclei with much larger numbers—up to 72 in some cases. These larger numbers, however, are nearly always multiples of 3, indicating that the subdivision of the chromosomes is an orderly process. The daughter chromosomes, moreover, that are formed by the subdivision of each of the original six, remain more or less closely associated as a "multiple complex," which behaves as a single individual in mitosis. It therefore appears that the three pairs of chromosomes "are made up of quite distinct individuals differing from each other to such a degree that chromatin split from one cannot associate itself with that from another pair . . . Chromosome individuality, alone, can account for these conditions."

Orderly fragmentation seems to be responsible for apparent variations in number in certain plants also. In *Œnothera scintillans* there are 15 chromosomes: seven pairs differing in length and one extra. Hance (1918*ab*) has observed that the somatic nuclei may have all the way from 15 to 21 chromosomes. Measurements show that the presence of more than 15 is due to a fragmentation of one or more of the longer chromosomes of the complement. The subdivision of chromosomes does not occur in the lineage of the reproductive cells.

The theory of chromosome individuality is strengthened, rather than weakened, by such instances of numerical variation as those described above. McClung emphasizes the point that the composition of a given chromosome can be fully understood only if something is known of its genetic history, for what appears as a chromosome may often be either an aggregation of two or three chromosomes, or, on the other hand, only a portion of the true chromosome individual. Such variations indicate the compound nature of the chromosome rather than lack of individuality.

Furthermore, it will be seen in a later chapter that it is not at all improbable that two homologous chromosomes may at times exchange corresponding segments with each other through the process known as chiasmatypy (p. 284). If this is the case, a given chromosome which can be followed as a distinct individual through successive generations may not always be composed of precisely the same parts. Hence the chromosome may be a persistent autonomous system whose several constituents may be replaced by homologous elements, rather than an unvarying unit.

**Conclusion.**—The following paragraphs are quoted from a discussion of the problem of chromosome individuality by McClung (1917):

> If it were possible for chromosomes to reproduce themselves and still preserve their physical configuration unchanged, there would probably be little question of their continuity and individuality—the demonstration would be self-evident. But it happens that the necessities of the case require that each newly produced chromosome should take part in the formation of a new nucleus, through whose activities the cell as a whole and each chromosome, individually, is enabled to restore the volume by the act of division. During this process the outlines of the chromosomes become materially changed and in their extreme diffusion can no longer be traced in many cases. Because of our limitations in observational power they appear to be lost as separate individuals and we are thus deprived of the simple test of observed continuity. Later, in the same cell, there reappears a series of chromosomes severally like those which seemed to disappear during the period of metabolic activity . . . Being organic, the chromosomes must change their form, they must suffer division of their substance, and they are obliged to restore this loss through metabolic changes. Since these changes of substance take place at surface contacts there is an obvious advantage in increased superficies and, in common with other larger structural elements, the chromosomes become extended and their substances are diffused. In this state their boundaries may not be well defined and this circumstance has been seized upon as a disproof of their continuity.
>
> Since it is not possible to observe directly the action of the chromosome we are obliged to make use of indirect evidence, seeking parallels between elements of structure and action in the chromosomes, and the mass effect of cellular action as exhibited in the so-called body characters. Such a method is justified by all other experience in tracing relations between structure and function in organisms, and while it apparently resolves the organism into parts of greater or less independence, has given us our best conceptions of it as a whole.
>
> It is my belief that the observed act of reproduction, by which the organization of the chromosomes is materially transmitted in each mitosis, together with all facts indicating extensive distribution of given conditions, definiteness of organization, uniformity of behavior and consistence of deviation from the normal, are so many clear indications of the individual character of the chromosomes. Transmutation of form, even to an extreme degree, cannot be held as a valid argument against a persistent individuality. A consideration of the criteria applied to larger organic aggregates well supports this view. Such

objects are said to possess individuality when they exhibit a more or less definite unity which is persistent and characterized by peculiarities of form and function. Most clearly defined is this individuality when it may be perpetuated through some form of reproduction to find expression in new units of similar character. The term does not connote unchangeability, and there may be fusions with more or less loss of physical delimitations, followed by separation, even after exchange of substance. The test of individuality is material continuity, but it does not necessarily involve complete or entirely persistent contiguity.

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## CHAPTER XI

# THE ACHROMATIC FIGURE, CYTOKINESIS, AND THE CELL WALL

In our account of the behavior of the chromosomes in mitosis only passing reference was made to the achromatic differentiations which play such an important part in the process of nuclear division. These achromatic structures will now be considered, together with the division of the cytoplasm which may or may not accompany nuclear division, and the formation of the cell wall, which is so conspicuous in plants.

### THE ACHROMATIC FIGURE

Recent researches on living cells have made necessary certain important modifications in our conceptions of the achromatic figure and its operation. There is still much uncertainty concerning the extent to which our ideas on many points must be revised. Probably an introduction to the subject and its literature may best be given by taking up first the phenomena observed in fixed preparations, which have formed the basis of the most complete descriptions, following this with an account of the newer observations on living cells and a discussion of the questions of the origin of the figure and its operation. The achromatic figure is usually regarded as including the spindle figure proper, the asters, and any centrosomal differentiations which may be present at the poles.

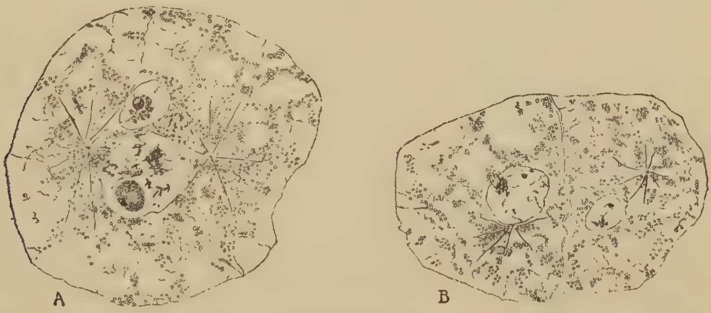

FIG. 68.—Centrosomes in fertilized egg just before nuclear fusion (*A*) and in young embryo (*B*) in *Preissia quadrata*. (*After Graham*, 1918.)

**The Centrosome.**—Centrosomes are characteristic chiefly of animals; in practically all types of animal tissue they have been found, at least in certain stages. In plants they occur in the thallophytes, in the spermatogenous cells of certain bryophytes and pteridophytes, and in one known case in the somatic cells of a bryophyte (Fig. 68). If the cilia-bearing organ, or blepharoplast, be regarded as a modified centrosome (see Chapter XIV), all motile cells (spermatozoids) of bryophytes, pteridophytes, and gymnosperms must be looked upon as possessing centrosomes. During the last decade of the nineteenth century the presence of centrosomes was reported in a number of angiosperms, but these cases have all failed to stand the test of subsequent more critical research.[1]

No single description can apply to all centrosomes, since they vary so widely in their morphology.[2] What may be called the "typical" centrosome, as seen in animals, lies in the cytoplasm (occasionally in the nucleus), and consists of two parts: a central deeply staining granule, or *centriole*, and a surrounding hyaline, alveolar, granular, or reticular mass known as the *centrosphere* (Fig. 69). Either of these elements may be present alone. The centriole may be single, but more commonly it is double as a result of division during the later phases of the previous mitosis; occasionally there are several centrioles, constituting together a "microcentrum." The centrosphere substance is often fairly abundant in resting cells, and is then frequently referred to as *archoplasm*. At certain stages, notably during mitosis, the centrosome is surrounded by a system of radiating rays known as the *aster*. The aster may sometimes show rather well-marked concentric zones, as well as one or more concentric series of granules about the centriole. It is questionable how far these are normal appearances, for Chambers (1917) asserts that some of them may be produced by subjecting eggs to abnormal environmental conditions. In plants, as will be seen further on, the centrosome is in general simpler than in animals, though in some cases it becomes fairly conspicuous and lies at the focus of a well-developed aster.

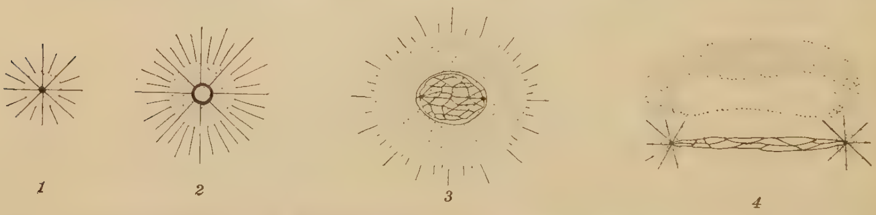

Fig. 69.—The formation of the initial spindle, or netrum, and its passage out of the centrosphere in the cleaving egg of *Crepidula*. (*After Conklin*, 1924.)

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[1] For a review of these cases, see Koernicke (1903, 1906).

[2] An exhaustive account of centrosomal differentiations is given by Heidenhain (1907). The terminology of the subject has long been in a confused state (see Wilson, 1900, 1925). In the present account we have chosen more or less arbitrarily a terminology which seems to have found favor with a number of recent writers, and which differs somewhat from that used in the first edition of this book.

The centrosome was discovered and described by Flemming (1875) and independently by van Beneden (1876). In 1887 van Beneden and Boveri, as a result of their researches on the threadworm, *Ascaris megalocephala*, independently concluded that the centrosome, like the nucleus, is a permanent organ maintaining its individuality throughout successive cell generations. They observed that, prior to cell-division, the centrosome divides to form two daughter centrosomes, which move apart to opposite sides of the cell and form the poles between which the mitotic figure is established; and further, that after cell-division is completed the centrosome included in each daughter cell does not disappear, but remains visible in the cytoplasm through the ensuing resting stage.

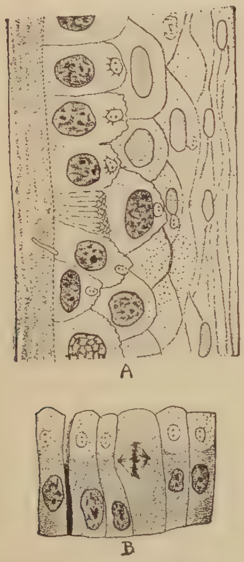

Fig. 70.—Centrosomes in epithelium of cornea of monkey (*A*) and of human gastric gland (*B*). (*After Zimmermann.*)

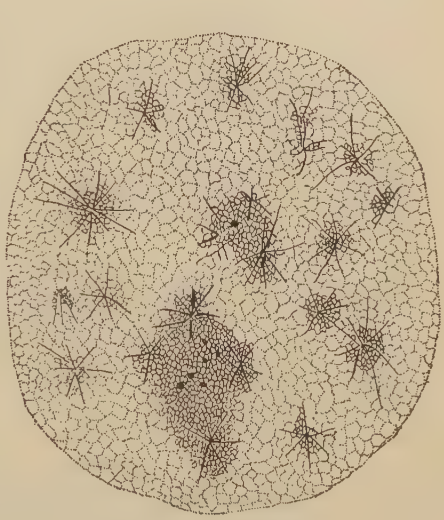

Fig. 71.—Artificial cytasters in the egg of *Arbacia*. (*After Morgan*, 1899.)

Because of this striking behavior at the time of cell-division the centrosome soon came to be known as "the dynamic center of the cell." The division of the centrosome was described in detail by Boveri (1901), Conklin (1902), and others. In the cleaving egg of *Crepidula* the centriole divides and gives rise to a minute spindle ("netrum") which moves out of the centrosphere, new asters differentiating about its poles (Fig. 69).

The above facts seemed to constitute ample ground for the conception of the centrosome as a permanent organ, but many obstacles have been found in the way of its acceptance as a theory of universal application. At certain stages in the history of many animal cells its presence cannot be demonstrated, and it is entirely absent from the tissues of higher plants. Furthermore, Mead (1898) and Morgan (1896, 1898) found that the formation of centrosomes with asters can be induced in the eggs of certain animals by treatment with NaCl and $MgCl_2$ solutions (Fig. 71), and it has been claimed that centrosomes so formed may function normally in the ensuing cleavages of the egg.

Conklin (1912*a*), however, shows that in *Crepidula* such "artificial cytasters" do not divide or take any part in mitosis. It is probable that no single conclusion can be drawn concerning this matter which will apply to all cases. There seems to be good evidence for the view that the centrosome in some tissues exists as a permanent organ, dividing at each mitosis and remaining visible through the metabolic stage, at least for a number of cell generations. In other cases it disappears at the close of mitosis, a new one apparently being formed just before the next mitosis. Thus Kowalski (1915) interprets the centrosome as a mass of material deposited at the meeting point of currents passing from the nucleus to the cytoplasm and *vice versa*. If more of this material is deposited than is used up during mitosis the centrosome is a permanent constituent of the cell; otherwise it is not. The fact that the formation of cytasters may be brought about by artificial means suggests that the regular appearance of the centrosome in successive mitoses is closely associated with regularly recurring physiological conditions, and that its presence in successive mitoses does not require an uninterrupted morphological continuity through the intervening stages. Its constant presence in some tissues probably indicates the continuity of some physiological function.

**The Achromatic Figure in Animals.**—Commonly the centrosome in the animal cell consists of a mass of centrosphere substance (archoplasm) with one or two centrioles in its midst, but without surrounding astral radiations. As the process of mitosis begins (Fig. 72), an aster, if not already present, develops about the centrosome. The centriole, if single, divides, and as the daughter centrioles move apart each is seen to be surrounded by its own aster. A small group of fibrils ("primary spindle," or "netrum") extends between them. The achromatic figure, made up of the asters and the spindle connecting them, is known at this stage and later as the *amphiaster*. As the centrioles continue to separate, the surrounding radiations increase in prominence; and as the nuclear membrane disappears some of them appear to grow into the nuclear region and establish connections with the chromosomes. Other fibrils continue to extend from one centriole to the other. The centrioles eventually reach polar positions and the chromosomes become arranged in the equator of the completed achromatic figure (Fig. 73).

During the anaphase the astral radiations remain conspicuous, but as the telophase progresses they gradually fade from view, except in those forms with more or less permanent asters. For some time con-

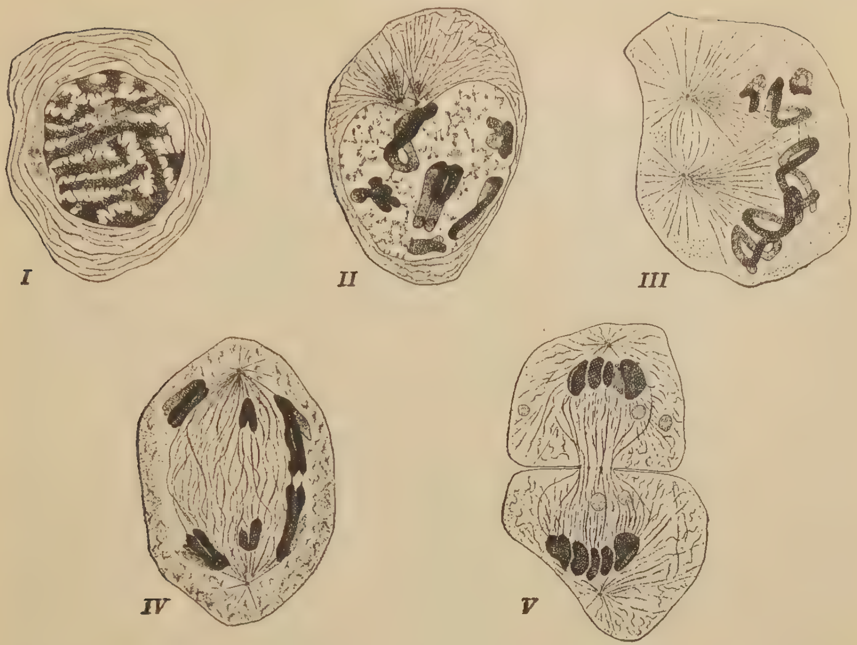

FIG. 72.—First meiotic mitosis in the spermatocyte of *Salamandra*. *I*, prophase: centrioles in centrosphere substance, which is spread out on nucleus. *II*, prophase: bivalent chromosomes formed; centrioles beginning to diverge; central spindle and asters developed. *III*, late prophase: nuclear membrane gone; centrioles moving apart; "fibrils attaching to chromosomes." *IV*, anaphase: connecting fibers prominent. *V*, telophase cytokinesis by constriction nearly completed; mid-body forming at equator. (*After Meves*, 1897.)

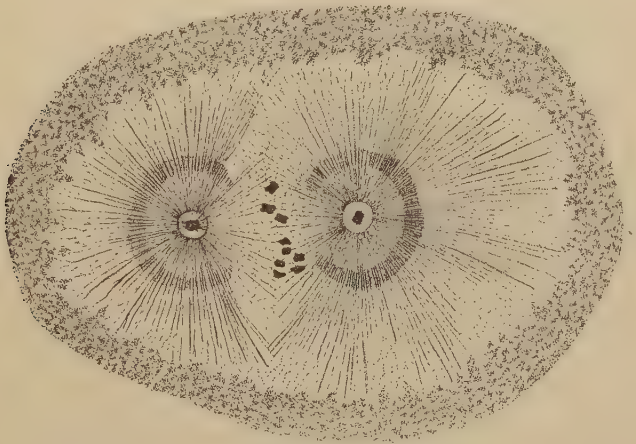

FIG. 73.—Achromatic figure in oöcyte of *Pisciola*. (*After Jörgensen*, 1913*b*.)

necting fibers remain visible between the daughter groups of chromosomes. In higher plants the partition separating the daughter cells is formed in close association with these fibers, but in animals the latter appear to play relatively little part in cytokinesis. Granules may be differentiated at the equatorial region, forming the so-called "mid-body," but the division of the cytoplasm is ordinarily brought about by the development of a cleavage furrow, as will be described in the section on cytokinesis.

**The Achromatic Figure in Plants.**—The achromatic figures of plants occur in two general types: with asters and centrosomes (amphiastral type), and without them (anastral type). The former type is found chiefly among the algæ and fungi. No centrosomes are known in seed plants. In the lower groups the figure is characteristically intranuclear. being completely established before the disappearance of the nuclear membrane. Cases are known in which the centrosomes themselves are intranuclear, but usually these bodies are situated in the cytoplasm against the nuclear membrane, so that the spindle portion of the figure lies within the nucleus and the asters in the cytoplasm. Intranuclear figures are also known in higher plants, as, for example, in the eggs of gymnosperms, but in such cases no centrosomes are present.

*Amphiastral Type.*—Among the fungi the achromatic figure has been most frequently studied in the ascomycetes.[1] In the ascus the mitotic process is essentially as follows (Figs. 74; 75, *A*, *B*). The centrosome, which in ascomycetes is often discoid in shape, lies against the nuclear membrane. As mitosis begins an aster usually develops in the cytoplasm about the centrosome, and the latter divides to form two daughter centrosomes. The primary spindle, if formed at all, does not persist. From each of the daughter centrosomes, which begin to move apart along the nuclear membrane, a group of fibers extends into the nucleus. The centrosomes finally reach opposite sides of the nucleus, and the two groups of fibers become arranged in the form of a sharp-poled spindle extending through the nucleus with the chromosomes at the equator. The nuclear membrane commonly remains intact until the chromosomes approach the poles at anaphase; it may then disappear, allowing the nucleolus, which has remained unchanged, to escape into the cytoplasm. Between the two densely packed daughter chromosome groups there extends a long strand of material derived from the achromatic figure (compare *Cladophora*, p. 234); this soon disappears and the two chromosome groups reorganize two daughter nuclei not separated by a wall.

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[1] Among the principal researches on mitosis in ascomycetes are those of Harper (1895, 1897, 1899, 1905), Faull (1905, 1912), Maire (1905*a*), Guilliermond (1904, 1905, 1911), H. C. Fraser (1908), Fraser and Brooks (1909), Fraser and Welsford (1908), Claussen (1912), W. H. Brown (1909, 1910, 1911), and Bagchee (1925). See also footnotes on p. 244.

Cytokinesis in fungi is commonly brought about by a cleavage furrow independent of the achromatic figure. After the final mitosis in the ascus the astral rays curve around and in some way become involved in the formation of the ascospore wall. Harper believed the walls to result from the actual lateral fusion of the rays, but this particular interpretation has been disputed by Faull and others. In his earlier papers

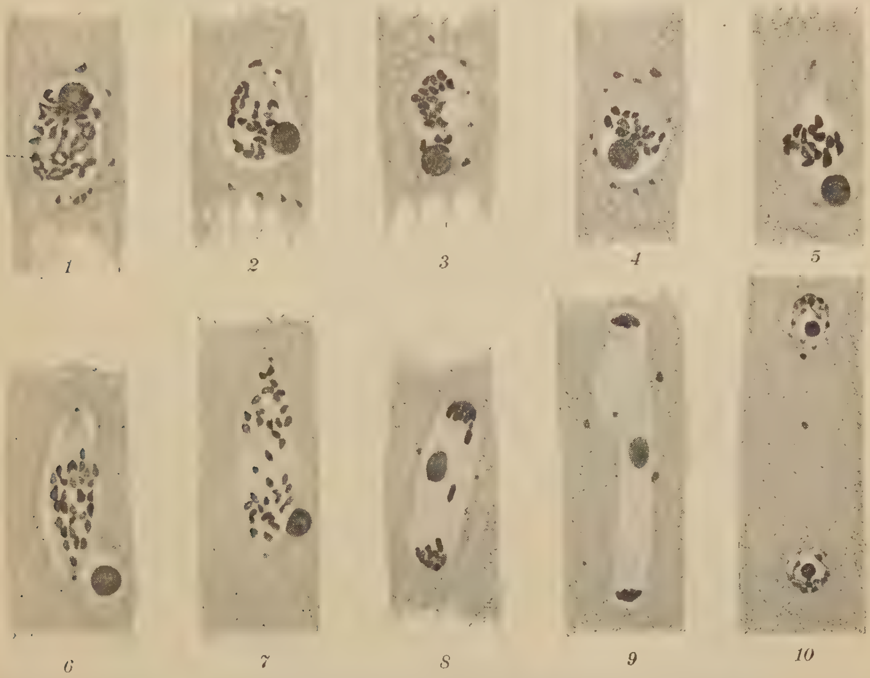

Fig. 74.—First meiotic mitosis in the ascus of *Pustularia bolarioides*. (*After Bagchee*, 1925.)

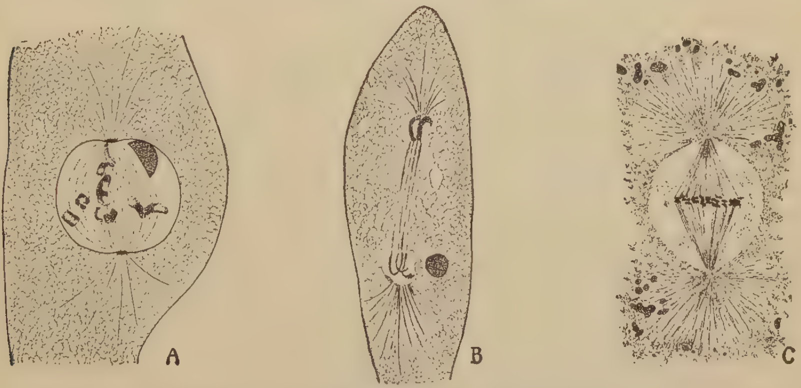

Fig. 75.—*A*, *B*, anaphase and telophase of mitosis in ascus of *Laboulbenia chœtophora*. (*After Faull*, 1912.) *C*, intranuclear mitotic figure in oögonium of *Fucus*. (*After Yamanouchi*, 1909.)

Harper treated the ascomycete centrosome as a permanent organ, and more recently (1919) he has spoken of it as a structure differentiated "as a region of connection between nucleus and cytoplasm and for the formation of fibrillar kinoplasm." In a basidiomycete, *Boletus*, the centrosomes present during the last mitosis in the basidium attach themselves to the basidium wall, mark the points of origin of the sterigmata, and eventually pass into the spores (Levine, 1913).

In certain algæ the achromatic figure has been found to bear a decided resemblance to that described above for the fungi. In *Dictyota dichotoma* (Mottier, 1898*b*, 1900) a curved rod-shaped centrosome lies against the nuclear membrane. As mitosis begins it divides into two which separate with their asters and occupy the poles of an intranuclear spindle figure (Fig. 76). In *Sphacelaria* and *Stypocaulon* the situation is similar, but workers do not agree as to the origin of the centrosome.[1] In the antheridium and oögonium of *Fucus* two sharply differentiated centrioles appear independently of each other, become surrounded by extensive cytoplasmic asters, and occupy the poles of an intranuclear spindle (Fig. 75, *C*) (Yamanouchi, 1909).[2] In *Polysiphonia violacea* (Yamanouchi, 1906) two centriole-like bodies are seen at opposite sides of the nucleus during the prophase. These later disappear, and their places are taken by two larger centrosphere-like structures (Fig. 76, *C*), which in turn fade from view during the later stages of mitosis.

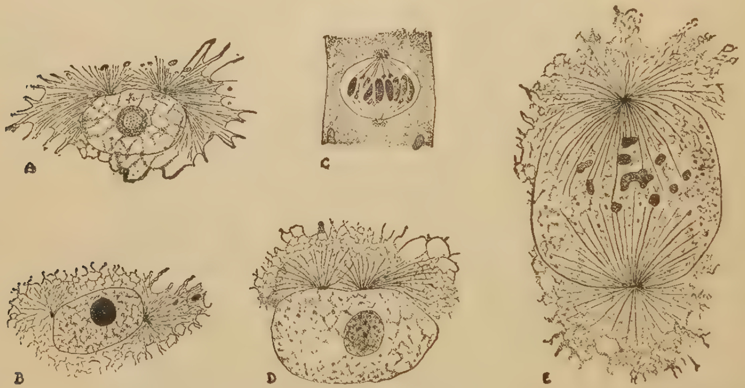

FIG. 76.—Centrosomes in algæ. *A*, *Stypocaulon*. (*After W. T. Swingle*, 1897.) *B*, *Stypocaulon*. (*After Escoyez*, 1909.) *C*, centrosphere-like bodies in *Polysiphonia*. (*After Yamanouchi*, 1906.) *D*, *E*, *Dictyota dichotoma*. (*After Mottier*, 1900.)

Achromatic figures with well-developed centrosomes also occur in the spermatogenous cells of bryophytes, pteridophytes, and certain gymnosperms. Although they are absent throughout the remainder of the life cycle, they play a conspicuous rôle in one or more of the mitoses preceding the differentiation of the spermatozoids. Several such cases will be described in the chapter on gametogenesis (Figs. 134–140).

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[1] J. Humphrey (1894), W. T. Swingle (1897), Strasburger (1900*a*), Escoyez (1909), Georgévitch (1922).

[2] Mitosis in *Fucus* was also described in the earlier papers of Farmer and Williams (1896, 1898) and Strasburger (1897).

*Anastral Type.*—In the vascular plants the achromatic figure is devoid of centrosomes and asters, except in the spermatogenous cells of forms with motile spermatozoids. In fixed material the figure in ordinary somatic cells appears to develop as follows. Toward the end of the prophase, when the chromosomes are in the form of thickened double spiremes, the nucleus commonly enlarges. It then begins to shrink, chiefly at the two sides facing the future spindle poles; and the region from which it retreats is seen to be occupied by two "polar caps" of hyaline substance (Fig. 77, *A*, *B*). The origin of this substance has long been a subject of controversy, but it is becoming increasingly evident, especially since the studies of Robyns (1924), that it is derived from the nucleus. This point will be discussed in a later section. As the nuclear membrane continues to contract more closely about the chromosomes the polar caps become correspondingly larger and gradually form a more definitely spindle-shaped figure. Within the cap substance fine fibers may appear, the degree of their prominence varying according to the method of fixation employed. Eventually the membrane disappears, and as the chromosomes become equatorially arranged in the spindle substance the fibers may be seen extending from the chromosomes toward the poles of the figure. In many cases the membrane disappears before there has been any noticeable shrinkage, the polar caps thus being smaller or absent. These different conditions strongly suggest that the hyaline

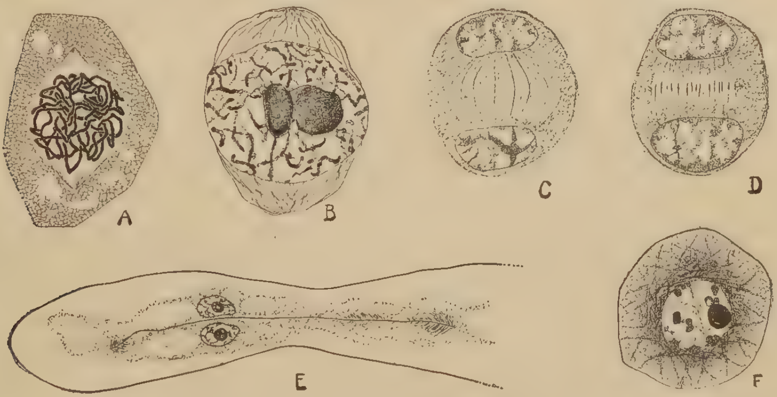

Fig. 77.—*A*, polar caps in *Nephrodium*. (*After Yamanouchi*, 1908.) *B*, same in *Marsilia*. (*After Berghs*, 1909.) *C*, *D*, telophase of mitosis in microsporocyte of *Pinus*, showing appearance of fiber thickenings through equator of achromatic figure. *E*, the continued extension of the partition wall after the completion of mitosis in the endosperm of *Physostegia virginiana*. (*After Sharp*, 1911.) *F*, "multipolar stage" in microsporocyte of *Acer Negundo*. (*After W. R. Taylor*, 1920.)

spindle substance is primarily karyolymph, the various cases differing in the amount of its exudation from the nucleus before the membrane disappears.

The spindle figure may terminate in a sharp point at each pole, or it may be a broad-poled structure which in extreme cases is as wide at the poles as at the equator. In case the preparation shows distinct spindle fibers, some of these are seen to extend from definitely localized points on the split chromosomes toward the poles, while other somewhat less prominent ones show no connection with the chromosomes. It is during the anaphase and the telophase that the latter fibers become most evident; in figures with many chromosomes they can often not be seen at metaphase. At the beginning of the telophase they may form a bundle no greater in diameter than the two groups of chromosomes, but as the daughter nuclei are reorganized the spindle substance extends laterally in the equatorial region and the fibers become correspondingly curved (Fig. 77, *C*). In this way arises the barrel-shaped *phragmoplast*, which in plants usually continues to widen, with the formation of additional fibers, until it comes in contact with the lateral walls of the cell.

While the above changes are taking place the new cell wall which is to separate the daughter cells begins to differentiate. As the phragmoplast widens the fibers become fainter near the nuclei and more prominent in the equatorial region, which suggests a flow of material toward the latter position. On the thickened fibers there now appear small swellings (Fig 77, *D*) which increase in size until they form a more or less continuous *cell-plate* between the daughter nuclei. This cell-plate is not itself the new wall; it represents rather the material which is to constitute the plasma membranes of the two daughter cells after being split into two layers, and between these layers the wall will develop. (See p. 215.) In certain cases, as in embryo sacs of angiosperms, such cell-plates may form and then disappear, leaving the nuclei in a common mass of cytoplasm. As the new wall develops the achromatic fibrils disappear completely, first near the nuclei and eventually near the wall. In a very broad cell the wall may begin to develop near the center of the phragmoplast while the latter is still growing toward the sides of the cell. In extreme cases cell-plate formation may still be seen in progress at the periphery after the fibers have completely disappeared in the central region (Fig. 77, *E*). Such is notably the case in the tangential divisions of elongated cambium cells (Bailey, 1919, 1920). When a cell contains a large central vacuole a portion of the parietal cytoplasm may gradually develop a strand across it, the mitotic figure then occupying this strand near the center of the cell (Goldstein, 1925).

The development of the achromatic figure has often been studied in the microsporocytes of seed plants. These cells are usually large and relatively free from one another at the time of their division, and present aspects somewhat different from those seen in ordinary tissue cells. In many of the earlier descriptions[1] of mitosis of sporocytes the formation of the figure was said to begin with the appearance of a felt-like mass of fine fibrils all around the nucleus; this was sometimes preceded by a stage characterized by radially arranged fibrils (Allen), or by a zone of granular "perikaryoplasm" (Lawson). The origin and fate of the weft of fibrils were variously conceived, but, in general, it was thought that these fibrils together with nuclear elements became the achromatic figure. Often they formed a number of radiating groups ("multipolar stage;" Fig. 77, *F*) before passing into the bipolar condition. In the four-lobed sporocytes of liverworts they are known to pass through a definitely four-poled stage (Farmer, 1894, 1895; Davis, 1899, 1901).

Devisé (1914, 1922) has more recently studied the achromatic figure in sporocytes, using *Larix*, which had frequently been studied by previous investigators. He finds that material fixed in the older reagents which, though good for chromosomes, are notoriously poor for cytoplasm, may show many of the appearances reported in earlier works, but that in cells treated according to the newer methods devised for the study of cytoplasmic structures much truer pictures are obtained. After a fixation (Benda) which comparison with living material shows to give the most nearly natural appearances, the cytoplasm of the sporocyte is homogeneous and contains many rod-like chondriosomes (Fig. 78). During the late prophase the chondriosomes move endwise toward the nucleus and lay themselves parallel with its membrane, forming a dense "perinuclear chondriosomal mantle." Improper fixation here gives the "radial" and "felted" stages so often described. The chondriosomal mantle remains intact throughout mitosis, its inner boundary marking the limit of the nuclear area. As the nuclear membrane disappears the chromosomes become grouped at the center of the nucleus, whose peripheral portion is then occupied by a substance representing karyolymph which has been rendered denser, probably through the influence of cytoplasmic fluid and possibly also by nucleolar matter. The important fact is that the spindle figure arises wholly from this peripheral intranuclear substance, the cytoplasm contributing no formed element. The fibers appear to be no more numerous than the chromosomes, and do not invade the nucleus from without; they appear first at the surface of the chromosomes and develop centrifugally until the completed spindle extends across the nuclear region with its poles at the chondriosomal mantle and surrounded on its sides by the intranuclear substance. The figure is bipolar from the beginning; multipolar appearances and extra fibers surrounding the spindle proper are held to be due to inadequate fixation. In the telophase the terminal portions of the spindle and the remaining intranuclear substance become two masses of hyaline fluid, in which the daughter nuclei are reconstituted; the hyaline substance of these nuclei is therefore continuous with that of the mother nucleus. The chondriosomes form mantles about the two nuclei. The cell-plate is not formed by a union of swellings on the spindle fibers, but first appears as a delicate layer in the homogeneous material between them.

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[1] Belajeff (1894*b*), Lawson (1898, 1900, 1903), Osterhout (1897), Mottier (1897), C. E. Allen (1903), Berghs (1905), Strasburger (1905*a*, 1908).

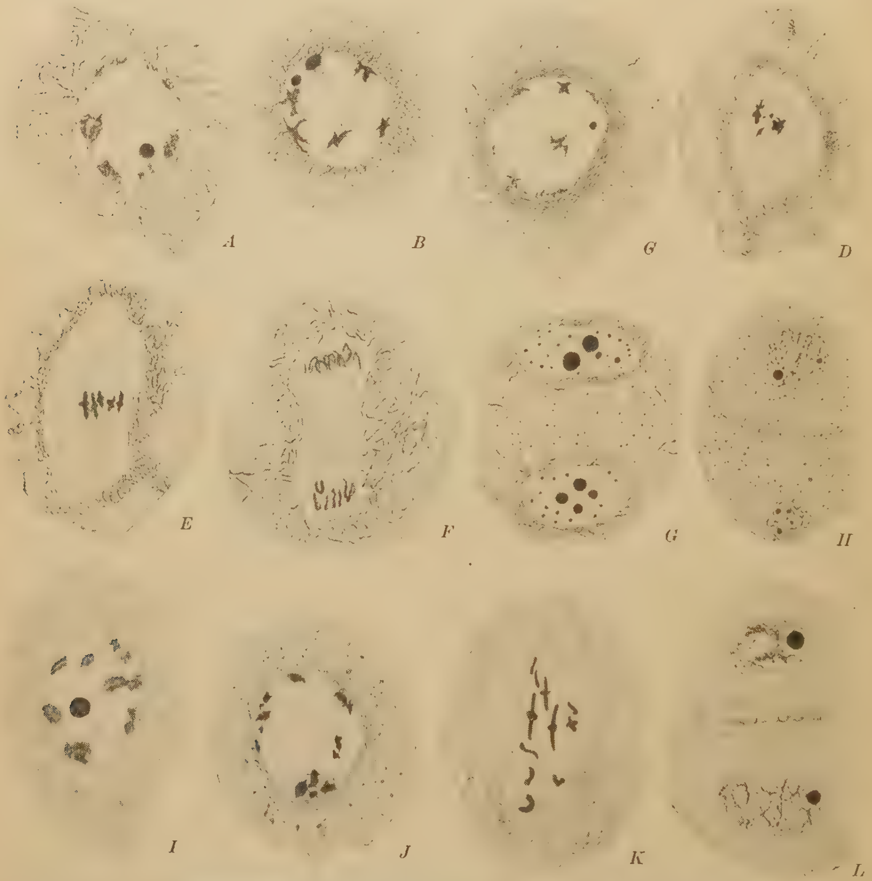

FIG. 78.—The development of the achromatic figure in the microsporocyte of *Larix europæa*. *A–H*, after fixation in Benda's fluid. *I–L*, after fixation in Flemming's fluid. Two successive stages of cytokinesis are seen in *L* and *H*. (*After Devisé*, 1922.)

**The Achromatic Figure in Living Cells.**—It is a notable fact that in all of the recent work on living cells the spindle figure appears as a homogeneous region with no evidence of a fibrous structure.[1] Its density is such that it can be moved bodily through the cytoplasm with dissecting needles (Chambers) or the centrifuge (Andrews, 1915). This is true of both the spindle figure proper and the aster. Although the aster is made up of both jellied strands and fluid rays, which are visible in the living state, it is dense enough to be rolled about with needles. The spindle of the microsporocyte of *Tradescantia* maintains its form even after the cytoplasm has been stripped off (Chambers and Sands). The viscosity of the spindle substance changes markedly during the successive phases of mitosis (Chambers, 1917; Heilbrunn, 1920*a*, 1921). Chambers has observed that the microdissection needle may be moved about in the spindle region of the insect spermatocyte without revealing any evidence of the presence of fibers, even when a chromosome is dragged completely out. In tissue cultures no fibers appear under usual conditions, but they may be caused to appear by making the nutrient medium acid (M. R. Lewis, 1923); and when the medium is again made neutral the fibers disappear. This reversible gelation may be repeated several times without killing the tissue. It is especially noteworthy that the mitotic process stops with the appearance of the fibers and is resumed when they disappear.

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[1] Chambers (1914, 1915, 1917, 1924), Chambers and Sands (1923), Sands (1923), M. R. Lewis (1923), Lewis and Lewis (1924).

**The Origin of the Achromatic Figure.**—Since many types of figures were observed by early workers it was natural that very divergent views should have been entertained concerning the method by which the figure is differentiated.[1] Some derived it wholly from the nucleus and some thought it wholly cytoplasmic, while others found that the figure seemed to occupy portions of both the nuclear and the cytoplasmic regions. When the remarkable behavior of the centrosome and its relation to the figure were made known, many adopted the theory that the centrosome in some way causes a morphological rearrangement of the preëxistent protoplasmic structure. According to particular views held regarding the ultimate structure of cytoplasm, the astral rays and spindle fibers were interpreted as oriented fibrils (Klein, 1878), distorted strands of a network (Lawson, 1911), or the walls of elongated alveoles (Bütschli, 1876); and it was thought either that the fibrils moved into the nucleus laterally when the membrane disappeared, or that an intranuclear linin reticulum became rearranged to form that portion of the figure (van Beneden, 1883; C. Williams, 1899). Similar ideas have also been more recently expressed.

Others interpreted the figure as a new differentiation of a special substance present in protoplasm, rather than a mere rearrangement of a structure already present. Boveri's archoplasm hypothesis in its earlier form (1888) was a prominent development of this idea. In many animal cells the centriole during the metabolic stage is surrounded by a conspicuous mass of substance appearing like an enormous centrosphere. Boveri called this substance *archoplasm*, and held that it gave rise to the entire achromatic figure, the spindle fibers and astral rays growing out from it like roots, to be withdrawn into the two daughter masses of archoplasm at the poles during the closing phases of mitosis. Each new cell thus received a portion of the archoplasm, a constantly present protoplasmic constituent. Boveri later (1895*b*) modified this hypothesis considerably when it was shown that the fibers appear to grow by the transformation of cytoplasmic substance at their ends. It remained evident, however, that the substance about the centriole was in some way specially concerned in the development of the achromatic figure.

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[1] For the early theories, see Wilson (1900, pp. 72–86, 316–329).

In the case of cells without centrioles or distinct masses of archoplasm, as in most plants, ideas of a special spindle substance were not so often suggested. Strasburger (1892, 1897*a*, 1898), however, advanced the view that the achromatic fibrils, as well as the ectoplast, centrosomes, cilia, and allied structures, are composed of a special fibrillar *kinoplasm*, which is concerned particularly with the motor work of the cell, and which is rather sharply distinct from the nutritive alveolar *trophoplasm*. This conception has been widely entertained (Davis, Němec, Chamberlain, and many others). Strasburger looked upon the nucleolus as a kinoplasmic reserve for the formation of the spindle, and others (*e.g.*, C. E. Allen, 1903) reported observations which seemed to indicate the participation of the nucleolus in this process. Later workers more commonly associate the nucleolus with the chromosomes.

Another general theory which has a broad observational basis is that the spindle figure arises as the result of an interaction of nuclear and cytoplasmic components at certain stages in the nuclear cycle. In *Allium*, for example, Nothnagel (1916) believes that the exosmosis of karyolymph through the nuclear membrane into the cytoplasm during the prophase causes the precipitation of fine fibrils which develop into the spindle, in much the same manner that interaction of karyolymph and cytoplasm is supposed by many to give origin to the nuclear membrane by precipitation. Tischler (1921–1922), who favors this interpretation, suggests that intranuclear figures are formed by the same kind of interaction, except that it occurs here within the nucleus as the result of an inward movement of cytoplasmic fluid. The plausibility of this general interpretation is increased by the fact that in the former case the nucleus usually shrinks as the fibrils appear, whereas in the latter case it enlarges; and also by the fact that all conditions between the two are known, the spindle being in various degrees partly intranuclear and partly extranuclear in origin.

Mention has been made of the work of Devisé (1914, 1922) on sporocytes, and of Robyns (1924) on somatic cells. In the *Larix* sporocyte, according to Devisé, the achromatic figure arises wholly in an intranuclear substance which appears to be the karyolymph altered in some way by cytoplasmic fluid after the shrinkage and disappearance of the nuclear membrane. Similarly, in the root cells of *Vicia* and *Hyacinthus* Robyns shows that as the nuclear membrane with the chromosomes contracts as a "chromosomic pouch" away from the two poles of the original nuclear area after a period of enlargement, it leaves behind the two polar caps of hyaline karyolymph, which allows the membrane to retreat by filtering through it (Fig. 79). These caps, which become the spindle cones, are thus topographically nuclear; they consist of karyolymph, which now lies between the shrunken nuclear membrane and the cytoplasm. Although the karyolymph increases in amount by the addition of fluid from the cytoplasm during the period of nuclear enlargement, the cytoplasm contributes no formed element to the developing achromatic figure. The observations of Robyns add further support to the view that the spindle is optically homogeneous in the natural state, visible fibers or lamellæ being results of improper fixation.

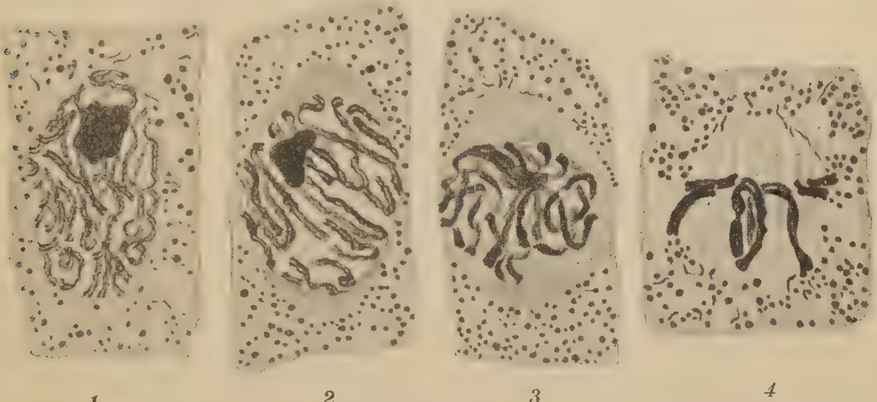

Fig. 79.—The development of the achromatic figure in the root tip of *Hyacinthus*. 1, stage of greatest prophasic nuclear enlargement. 2, polar caps present, due to shrinking of nuclear membrane. 3, nuclear membrane partly gone; caps about to develop into spindle cones. 4, spindle cones established; metaphase. Note that the chondriosomes do not invade the spindle area. (*After Robyns*, 1924.)

In the microsporocyte of *Elodea* the drawings of Santos (1924) indicate that the spindle figure is of intranuclear origin, cytoplasmic influence being suggested by the fact that fibers do not appear until the nuclear membrane disappears (Fig. 192). In the oöcyte of an insect, *Acroschismus Wheeleri*, S. H. Schrader (1924) finds that a fusiform mass of spindle substance develops about each of the eight tetrad chromosomes, these eight elementary spindles then becoming parallel to form the first maturation figure. In this peculiar case, also, the coöperation of a cytoplasmic fluid is probable, for the elementary spindles begin to develop within the karyolymph during a temporary fading out of the nuclear membrane.

It appears not improbable that all cases of spindle formation can be harmonized on the basis of the hypothesis that during the prophase the nuclear membrane undergoes alterations in permeability, or even complete disappearance, allowing an interaction between the karyolymph and some cytoplasmic constituent; hence the actual spindle substance is essentially a somewhat modified karyolymph. According as the direction of movement through the membrane region is chiefly inward or outward, the spindle figure will be chiefly "intra-nuclear" or "extra-nuclear." It may be that the permanent centrosphere or archoplasmic mass of certain animal cells should be interpreted as a visible accumulation of the cytoplasmic constituent which interacts with the karyolymph, this constituent being more generally diffused in other cells. The centrioles would accordingly be looked upon as structures more or less sharply differentiated according to the degree of localization or polarization of the movement of the interacting constituents. The prominence of the astral rays would depend upon the extent of the cytoplasmic region involved in movements of material to and from the poles of the spindle figure, and the degree to which such currents modify the cytoplasm through which they pass. It is, of course, difficult to determine how far the development of the aster, like that of the spindle figure proper, is dependent on direct nuclear influence.

Here may be recalled the statements made in the preceding section regarding the appearance of the achromatic figure in living cells. The rays of the aster are distinctly visible, and it has been shown by Chambers (1921*b*, 1924) that in echinoderm eggs they represent fluid paths separated by regions of jellied granular cytoplasm, thus confirming the widespread view that the aster is primarily an expression of streaming movements in the cytoplasm. The rays merge into a central mass of hyaline fluid which may in some cases begin to accumulate before the cytoplasm becomes sufficiently jellied to reveal the centripetal channels.

The situation is somewhat different in the case of the so-called "fibers" of the spindle figure proper. These are not visible in the uninjured living cell, but may be made to appear by agencies causing gelation or coagulation. The inference that they are wholly fixation artifacts is, however, in all probability too extreme. It is true that the coarsely fibrous appearance in fixed spindles is not natural, and that the better the fixation the more vague the fibers become. But there are certain facts which indicate that the appearance of fibers on fixation is in some measure dependent on actual local differences in the untreated spindle substance. It has been found, for example, that the principal fibers develop in definitely localized positions, which seem clearly to be determined by a special differentiation at that particular portion of each chromosome which is soon to move first toward the pole. The most plausible hypothesis concerning the nature of the local condition in the spindle substance opposite this portion of the chromosome—the condition which is revealed as a fiber or group of fibers by fixation—is that it is a line of streaming extending polewards from the chromosome. Such currents in this region of the cell have been detected by students of cytokinesis (p. 209). The projections on the chromosomes at the beginning of the anaphase, which were once interpreted as results of the contraction of attached fibers, have much more the appearance of a localized flowage of the semi-fluid chromosome substance, especially in the first meiotic division before the chromosomes have begun to move as wholes (Fig. 63, *D*, *E*). In harmony with this conception of an intensified streaming at these regions is the fact that the "fibers" are more distinctly differentiated here than elsewhere in the spindle area. Again, in the intranuclear spindles of algæ and fungi (Figs. 74–76) the fibers appear in a position definitely related to the centrosome, indicating that the latter is, as Harper says, "a region of connection between nucleus and cytoplasm"—a region through which pass currents made visible by fixation. The progressive lengthening of the fibrils seen in successively fixed stages, whether the apparent growth is from the centrosomes or from the chromosomes, probably indicates a gradual extension of the region of streaming, and not merely an increased tendency to gel. In figures without centrosomes the irregular arrangement of fibers formed at early stages would accordingly indicate a less definite polarization of streaming, the bipolar condition developing later (Figs. 78, 113).

That the local differences in the spindle substance are regions of intensified streaming in a physically nearly uniform material, rather than jellied strands or channels through a jelly, is suggested by their invisibility and their failure to offer resistance to the microdissection needle. In the aster the rays are visible, for they are hyaline fluid paths through a granular jelly (Chambers), but in the spindle proper the paths of flow are invisible because they are less definitely delimited regions in a hyaline fluid of nearly uniform physical consistency. Fixation in some way causes a differential gelation of the currents and the less actively moving regions. What represent the spindle fibers in the living cell may be likened to the indefinitely delimited currents frequently observed in pools of water; if the water is very clear, such currents may be invisible, but they are revealed when the pool becomes partly frozen.

**The Mechanism of Mitosis.**—It has always been tempting to speculate upon the mechanical factors involved in the remarkable process of mitosis. Although the problem is still very far from solution, it will be of service to review briefly some of the suggestions which have been made.[1] One of the simplest and most widely accepted theories was that of fibrillar contractility proposed by Klein (1878) and van Beneden (1883, 1887), according to which the chromosomes were supposed to be dragged apart by the contraction of two opposed groups of spindle fibers. Many observations were cited in its favor, and elastic models were made to illustrate the supposed contraction and its results (Heidenhain); but evidence subsequently brought forward by Hermann (1891), Drüner

[1] See the reviews by Wilson (1900, 1925) and Tischler (1921–1922).

(1894, 1895), Calkins (1898), and many others led to the general restriction of the rôle of contractility, until it became apparent that this factor must be one of very minor importance. This is especially evident in view of what is now known of the spindle figure in living cells.

The striking resemblance between the achromatic figure and the lines of force in an electromagnetic field naturally led to attempts to account for mitosis on the basis of electrical principles. Several investigators, working with various chemical substances, succeeded in modeling fields of force that illustrated graphically the changes supposed to take place in mitosis. In later years the electromagnetic interpretation was again brought into prominence by Gallardo, Hartog, and Prenant. At first Gallardo (1896) believed the two spindle poles to be of unlike sign, but later (1906), as the result of the researches of Lillie (1903) on the behavior of nucleus and cytoplasm in the electromagnetic field, he concluded that the chromosomes and the cytoplasm carry charges of unlike sign. The daughter centrosomes repel each other and move apart because of their like sign, the spindle poles being of like sign also. The movement of the chromosomes to the poles he held to be due to the combined action to two forces: the mutual repulsion of the similarly charged daughter chromosomes, and the attraction between the oppositely charged centrosome and chromosome.

The fact that the two centrosomes and hence the two spindle poles are electrically homopolar (Lillie) and alike osmotically at once makes it apparent that the miotic figure does not represent an ordinary electromagnetic field, for in the latter the poles are of unlike sign—the field is heteropolar. It has consequently been suggested by Prenant (1910) and Hartog (1905, 1914) that the mitotic figure is the seat of a special force, analogous to electrostatic force but not identical with it, which is peculiar to living organisms. This new force they call "mitokinetism." Much discussion has centered about the possible rôle of electrical forces in mitosis, and many kinds of normal and abnormal mitotic phenomena have been cited as evidence for various views. Meek (1913) asserts that the only generalization which is at present possible is the negative one that "the mitotic spindle is not a figure formed entirely by the action of forces at its poles."

A hypothesis based on the conception of the centrosome as an oscillating body has been proposed by Lamb (1908). Bjerknes (1900) had shown that in a fluid medium an oscillating body will repel other bodies lighter than the medium and attract those which are heavier. Lamb applied this to mitosis, suggesting that the chromosomes first collect at the equatorial plane because of the repulsive force of the two oscillating centrosomes, and later, through an increase in their density, move toward the centrosomes. In reply to the objection that there is no evidence for an increase in the density of the chromosomes, Cannon (1923) pointed out that the medium is known to alter its viscosity during mitosis, and that it is the relative density of the medium and chromosomes, rather than the absolute density of either alone, that is of importance. Cannon discusses the application of Lamb's hypothesis to a variety of other cell phenomena.

Osmosis has been used in a special way by Lawson (1911*b*) to account for certain mitotic phenomena. The exosmosis of karyolymph which causes the nucleus to shrink also sets up a tension in the cytoplasmic reticulum, the achromatic figure being the expression of this tension. Although the chromosomes move along these tension lines toward the poles, they are not actually drawn by them, for the tension, expressed in the connecting fibers, remains until well into the telophase. The view that the fibers serve as guide lines rather than active agents in chromosome movement has been widely held. Although osmosis is rightly emphasized as a factor of probable importance, the interpretation of the spindle figure as a distorted cytoplasmic reticulum no longer seems valid.

Special significance has been attached to streaming by students of mitosis ever since Bütschli, Fol, and others showed many years ago that currents usually exist in the protoplasm. The more recent researches of both microdissectionists and other cytologists (*e.g.*, Kowalski, 1915) have yielded further evidence for the importance of this factor. Special emphasis therefore has been placed on streaming in the foregoing discussion of the origin of the achromatic figure. Its relation to chromosome movement is further suggested by phenomena observed in cells subjected to the influence of chloral hydrate and other anesthetizing agents. Němec (1910), Sakamura (1920), van Regemorter (1925), and others have observed that in such material (chiefly root tips) the chromosomes of dividing cells behave with an irregularity which varies with the strength of the dose. After very heavy doses they may show little or no movement; after moderate doses they pass irregularly toward two, three, or more regions in the cell; after very light doses their behavior may be nearly normal. Chloralized cells characteristically show no spindle fibers; a hyaline material evidently representing spindle substance is seen about the chromosomes, but no definite figure is developed. Němec and Sakamura attribute such movements of chromosomes in the absence of spindle fibers to protoplasmic streaming induced by the experimental agent, which is in harmony with G. Ritter's (1911) observation that the nucleus may sometimes be displaced by streaming induced by the wounding of near-by cells. The experiments of van Regemorter indicate that the failure of the spindle substance to develop a regular figure in chloralized tissue is due to a destruction or impairment of the cell's polarity, the recovery from the effect of the reagent involving a return to the properly polarized condition. The significance of streaming in chloralized cells with reference to normal chromosome movement has been questioned; but in view of the many observed gradations between normal and abnormal movement, and the fact that it is now practically certain that spindle fibers do not represent lines of traction, the simplest hypothesis is that, in general, a streaming of the material in which the chromosomes lie is an important factor in determining their movement. In some cases lines of such streaming are polarized and sufficiently localized to become visible upon fixation, whereas in others they are not. This is further indicated by such cases as that of *Cladophora* (T'Serclaes, 1922), in which the chromosomes regularly divide and separate in normal mitosis without the appearance of any achromatic fibrils.

The reasons for polarized streaming movements in the spindle region at the time of mitosis are as obscure as those responsible for protoplasmic streaming at other periods. Cytologists are only beginning to see clearly a relation between such movements and the phenomena of gelation, alteration in surface tension, electrical effects, and changes in the permeability of membranes. In no one of these many phenomena alone is the key to the problem of mitosis to be found; all of them are in some manner involved in the process. In spite of the confidence that some progress has been made and that new methods are to teach us much, we shall probably not soon have an adequate understanding of the complicated series of changes called mitosis.

## CYTOKINESIS

The subdivision of growing and differentiating masses of protoplasm into cells is accomplished in several ways, involving the development of cleavage furrows, the accumulation of masses of vacuole substance or other material in certain regions, the formation of membranes, and the differentiation of cell-plates in the equatorial plane of the spindle figure at the close of mitosis. The division of the extra-nuclear protoplasm is known as *cytokinesis;* the division of an ordinary uninucleate cell thus involves both cytokinesis and karyokinesis.

**By Furrows and Vacuoles.**—*Thallophytes.*—The cleavage of plasmodial masses is most commonly brought about by the formation of furrows, with or without the coöperation of vacuoles. It is well illustrated in the sporangia of myxomycetes and certain fungi, as shown by the researches of Harper and others.[1] In *Fuligo* cleavage furrows begin to develop at the peripheral membrane of the young sporangium and gradually extend inward, cutting out multinucleate blocks which are subdivided by further furrowing into uninucleate spores. In *Didymium* the spores are delimited in a similar way by furrows which begin to develop both at the periphery and along the young capillitium filaments in the midst of the protoplasm. In *Rhizopus* the furrows develop from the peripheral membrane (Fig. 81, *A*) and from the columella. In the sporangia of *Achlya, Saprolegnia,* and *Olpidiopsis* the furrows start from a large central vacuole. In *Phycomyces* vacuoles appear in the protoplasm, become stellate in form, and cut out spore masses with from one to twelve nuclei each (Fig. 81, *B*). Such vacuoles function together with peripheral furrows in *Pilobolus* and *Circinella.* In the sporangia of the phycomycetes the columella is separated from the rest of the sporangium by a dome-shaped layer of vacuoles which coalesce and form a continuous partition between the two regions.

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[1] Harper (1899, 1900*a*, 1914) on *Synchytrium, Pilobolus, Sporodinia, Fuligo,* and *Didymium;* D. B. Swingle (1903) and Moreau (1913) on *Rhizopus* and *Phycomyces;* Rothert (1892) and Schwarze (1922) on *Saprolegnia* and *Achlya;* Davis (1903) on *Saprolegnia;* Rytz (1907) on *Synchytrium;* Schwarze (1922) on *Circinella.*

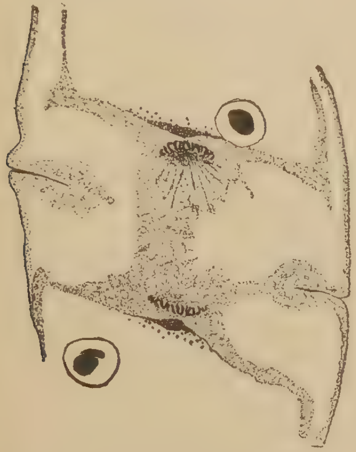

Fig. 80.

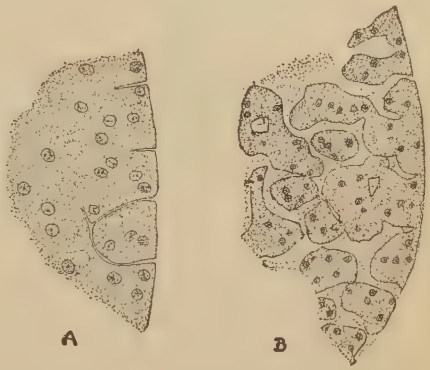

Fig. 81.

Fig. 80.—Cytokinesis by furrowing in *Closterium.* Only the central portion of the cell is shown. (*After Lutman*, 1911.)

Fig. 81.—*A*, cleavage furrows beginning to develop at periphery of sporangium of *Rhizopus nigricans. B*, cleavage in the sporangium of *Phycomyces nitens;* intersporal substance in the angular furrows. (*After D. B. Swingle*, 1903.)

Conditions very similar to those in the fungi are found in certain algæ.[1] In *Hydrodictyon*, for example, the multinucleate protoplasm lining the wall of the large cell is cut up into uninucleate swarmers by cleavage furrows, which appear to begin their development from the cell and vacuole membranes (Timberlake, 1902) and from cleft-like vacuoles (Klebs, 1891). Often the furrows thus developing inward from the cell membrane are very narrow, as in the vegetative and reproductive cells of *Polysiphonia*, described by Yamanouchi (1906). Such furrowing in many algæ is regularly incomplete at the center, leaving a large communicating pore, which is often occupied by a chromatic granule. In some cases the wall substance seems to take the lead in developing the furrow, a "girdle wall" developing centripetally as a ring-like ingrowth from the lateral wall, apparently pushing the protoplast before it. In *Cladophora*, for example, Brand (1908) has shown that the accumulation of slimy material seen against the wall as the process begins (Fig. 82, *B-F*) is probably swollen wall substance, rather than cell sap as Strasburger thought. In *Cladophora* this girdle wall formation seems to be independent of nuclear division, but in uninucleate cells, as in *Spirogyra* (Strasburger, 1875) and *Closterium* (Lutman, 1911), it occurs immediately after nuclear division (Figs. 82, *A*; 80). The processes commonly known as "division by constriction," as in unicellular algæ, and "budding," as in yeast cells, conidia, and basidiospores, may be regarded as special cases of cytokinesis by furrowing.

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[1] For literature pertaining to algæ, see Oltmanns (1922–1923).

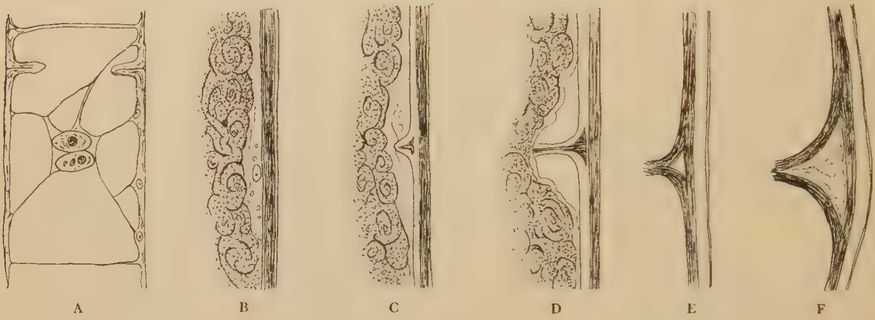

FIG. 82.—*A*, girdle wall developing in *Spirogyra*. (*After Nathanson*, 1900.) *B–F*, five stages in the development of the girdle wall in *Cladophora*. (*After Brand*, 1908.)

*Sporocytes.*—The microspore quartets of most vascular plants fall into two types as regards the shape and arrangement of the spores. If no permanent wall is formed after the first meiotic mitosis, the four spores are delimited by walls appearing simultaneously after the second mitosis; such spores when first formed commonly have the tetrahedral form, though this is not always the case. If the first mitosis is followed immediately by the formation of a permanent wall through the equator of the sporocyte, each hemisphere being divided by a wall after the second mitosis, the quartet is said to be of the "bilateral" type.[1] Other types of quartets are also known.

The method by which the partition walls are formed in the sporocyte varies rather widely in different groups. It was for some time supposed that angiosperm microsporocytes were divided by the formation of cell-plates through the mitotic spindles, but the researches of C. H. Farr (1916, 1918, 1922) and W. K. Farr (1920) have shown that furrows developing inward from the periphery are chiefly responsible for cytokinesis here, at least in the case of simultaneous division (quadripartition) to form tetrahedral spores. In *Nicotiana*, for example, the four microspore nuclei after the second mitosis all become connected by achromatic fibrils (Fig. 83). The two sets of connecting fibers of the second mitosis may persist, four new sets being added, or the two may disappear, six sets being developed anew. Although some sporadic thickenings may appear on these fibers, they have nothing to do with the formation of the separating walls, there being no centrifugally growing cell-plates such as are seen in the cells dividing by the cell-plate method. Constriction furrows appear at the periphery and grow inward until they meet at the center, dividing the protoplast simultaneously into four spore cells. In some cases (*Nelumbo*) the furrows are exceedingly narrow, appearing much like cell-plates. As they grow inward they seem simply to cut through any fibers which they may encounter.

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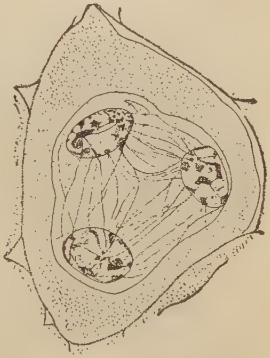
[1] Although either the "simultaneous" or the "successive" mode of division may tend strongly to predominate in certain groups of plants, there are so many exceptions to rules and so much variation that the character is of very restricted taxonomic value. See Täckholm and Söderberg (1917, 1918), Söderberg (1919), Palm (1920), Suessenguth (1921), Stenar (1925), and Coulter and Chamberlain (1903).



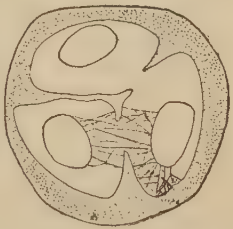


FIG. 83.—Cytokinesis by furrowing in the microsporocyte of *Nicotiana*. (*After Farr*, 1916.)

Meanwhile there develops just within the original sporocyte membrane a mass of gelatinous material known as the "special wall." This increases in thickness and follows the furrows inward, forming a sort of matrix in which the spore cells lie while their elaborate coats are being differentiated (see p. 220). The source of this material is not altogether clear. By some it has been attributed to a colloidal swelling of the secondary layers of the sporocyte wall (Farr); but Gates (1925), working with *Lathræa*, in which the sporocytes do not round up before cytokinesis, concludes that it is secreted by the protoplasm, first from the surface generally and later from the sides of the advancing furrows. Eventually the sporocyte wall and the material separating the four microspores disappear, leaving the spores free.

Cytokinesis in the microsporocyte of *Melilotus alba* as described by Castetter (1925) is of special interest in that vacuoles appear to play a conspicuous part in the process (Fig. 84). After the second mitosis, hyaline areas develop in the regions between the four nuclei, apparently as a result of a movement of granular material from these regions toward the nuclei, accompanied by an extrusion of liquid into vacuoles. These vacuoles fuse to form larger ones which nearly separate the protoplasm into four masses. Furrows originating at the surface then grow inward, soon meet the vacuoles, and complete the cleavage of the protoplast.

With regard to the wall, Castetter finds that as the sporocyte rounds up it secretes a large mass of callose, within which a second mass of denser callose is secreted as a special wall during the early stages of cytokinesis. This special wall extends inward with the growing cleavage furrows through further secretion of callose, and eventually completes the partitions between the four microspores. Finally, after the coats of the microspores have been developed, the sporocyte wall and the special wall break down, liberating the spores.

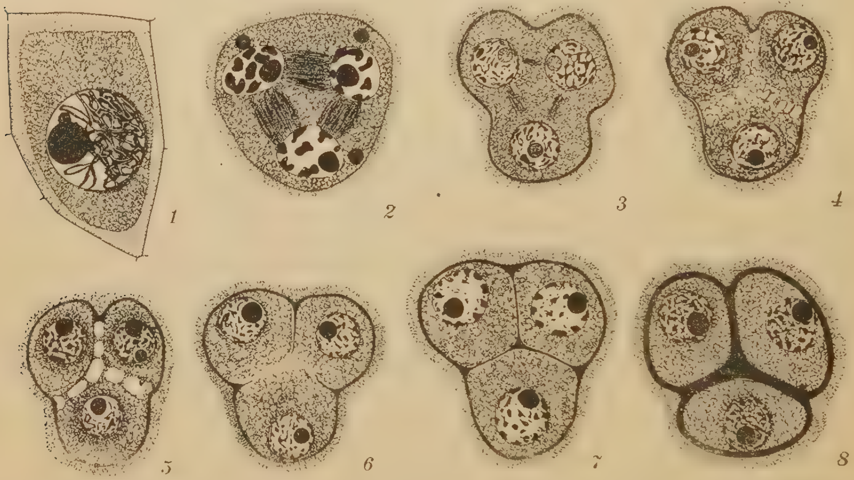


FIG. 84.—Cytokinesis in the microsporocyte of *Melilotus*. 1, prophase of first meiotic mitosis; callose (uniformly stippled) being secreted by the protoplast. 2, telophase of second mitosis. 3, special wall (black) and furrows appearing. 4, 5, vacuoles forming between nuclei. 6, special wall extending inward. 7, special wall extensions have met at center. 8, thickened special wall complete. (*After Castetter*, 1925.)

In *Magnolia* Farr finds a case in which bilateral quartets are formed by furrowing, rather than by cell-plates as might be expected. As in *Nelumbo*, a transitory cell-plate may be differentiated, but it plays no part in cytokinesis. After the first mitosis a cleavage furrow starts to form, but its development is arrested until after the second mitosis, when it resumes its growth and forms a partition through the equator of the sporocyte. At the same time additional furrows subdivide the two hemispheres, delimiting the four microspores. Farr states that no case of bipartition by furrowing, which is so common in animals, is known in the higher plants. Bipartition begins in *Magnolia*, but owing to the suspension of the furrow's growth the division is eventually by quadripartition.

Cytokinesis by membranes and cell-plates also occurs in sporocytes, and will be described later.

*Animals.*—Cytokinesis in animals is most commonly accomplished by furrowing (Figs. 72, 85), and has been followed most closely in segmenting eggs. In small eggs, such as those of worms, the daughter cells (blastomeres) round up and become more or less spherical, whereas in larger eggs, such as those of frogs, a narrow cleavage furrow appears at one pole and develops through the egg without altering the shape of the latter, so that the first two blastomeres have the form of hemispheres. In many cases the cleavage is superficial, not extending entirely through the yolk-laden egg.

So far as known there are no animal cells that are divided by cell plates of the type found so commonly in plants. As noted in a previous section, there is often a slight differentiation (the "mid-body") at the equator of the achromatic figure in the telophase, but it plays no part in cytokinesis. In the spermatogonia of certain insects Janssens (1924) finds a cell-plate-like differentiation which appears to represent a region of protoplasmic continuity rather than a structure concerned in cytokinesis.

Vacuoles may also function in cytokinesis in animals. In certain epithelial tissues, for example, which begin their development as multinucleate plasmodial masses, vacuoles appear in the cytoplasm and subdivide the mass into uninucleate cells, which, however, maintain protoplasmic continuity (Fig. 15, *D*).

*Mechanism of Furrowing.*—Experiments with dividing cells, chiefly animal eggs, have led to the identification of some of the factors involved in the development of cleavage furrows. Many years ago Bütschli (1876) advanced the view that cytoplasmic currents flowing toward the centrosomes lead to the production of a relatively high surface tension at the equator of the cell, this, in turn, bringing about furrowing through this region. Evidence favoring this interpretation has been afforded in the researches of McClendon (1910, 1913), Spek (1918, 1920*b*), Cannon (1923), and Just (1922), who have shown that the surface tension is higher at the cleavage plane than at the poles. Spek imitated furrowing and division with oil and mercury droplets in water, and showed that by lowering the surface tension at two poles of the droplet the relatively higher surface tension at the equatorial region could be made to bring about the constriction and fission of the droplet. In both droplet and

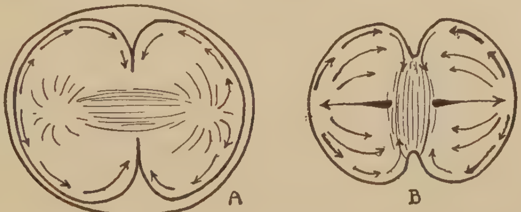


FIG. 85.—Diagram of streaming and furrowing in the egg of *Rhabditis pellio* (*A*) and an oil droplet (*B*). (*After Spek*, 1918*a*.)

dividing nematode egg he found streamings such as Erlanger (1897) had described in the egg: an axial movement polewards to the region of low surface tension and a superficial streaming toward the equatorial region of higher surface tension, the streams turning inward at the furrow (Fig. 85).

Closely associated with such streaming and surface tension phenomena are certain periodic alterations in the viscosity of the egg substance, as shown by Heilbrunn (1915, 1921) and Chambers (1917, 1919). In the living echinoderm egg it is found that the two asters developed in connection with the first cleavage division are regions in which the protoplasm has become decidedly more viscous, the peripheral and equatorial regions at the same time showing a high degree of fluidity and active streaming such as has been mentioned above. As the growth of the two semi-solid masses results in a slight elongation of the egg, a cleavage furrow develops in the more fluid region separating them, after which the asters revert to a less viscous state. Chambers has shown the dependence of the location of furrows on local differences in viscosity by a number of interesting experiments. If a dividing egg be cut in two obliquely through the two asters the pieces will continue to cleave along the fluid equatorial plane if the asters continue in the semi-solid state; but if the asters revert to the fluid condition, as often happens as the result of rough handling, the cleavage furrow is obliterated, and the pieces produced by the cut divide symmetrically at the next cleavage (Fig. 86). If the formation of a furrow at the first mitosis is prevented by mechanical means, furrows are developed between all four asters in

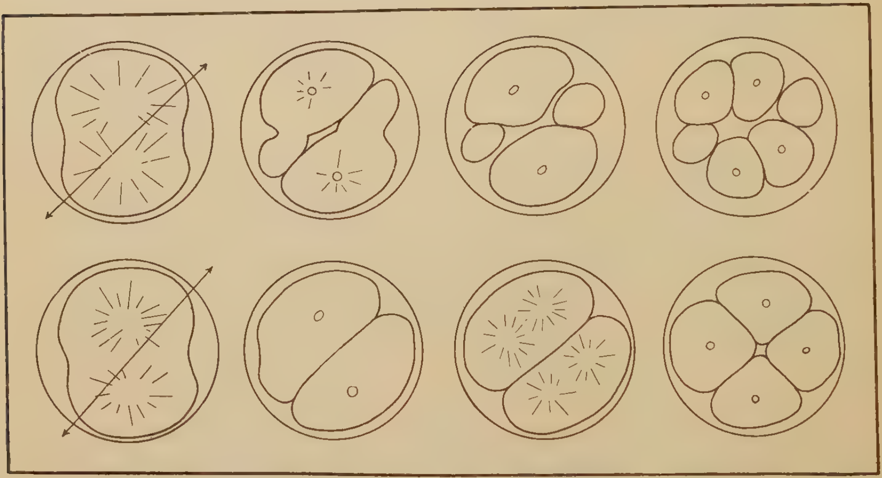


Fig. 86.—Diagram showing the effect of bisecting a cleaving echinoderm egg. First row: without disappearance of amphiaster. Second row: with disappearance of amphiaster. (*After Chambers*, 1919.)

the second mitosis, cleaving the egg simultaneously into four blastomeres. Such observations indicate a close connection between cytokinesis in eggs and the temporary differentiation of semi-solid regions in the cytoplasm, and throw considerable light on the question of the true nature of the achromatic figure.

Alterations in surface tension and viscosity, together with protoplasmic streaming, are obviously important factors in cytokinesis of certain types, but comparatively little is known about the initial causes of these phenomena. That they are in some way associated with changes in the permeability of protoplasmic membranes seems clear from the work of Spek and others on animal eggs and of Stălfelt (1921) on plant cells. A promising beginning has been made on the problem of the mechanism of cytokinesis, but its solution lies far in the future.

**By Differentiation of Metaplasm.**—Similar in appearance to vacuoles bringing about cytokinesis are the masses of metaplasm (Rohde; see p. 76), which differentiate in certain young tissues (cartilage, bone) in the early plasmodial stage, and gradually mark out the cells (Fig. 15, *E*). Rohde (1923) lays emphasis on the fact that this metaplasm or living ground substance is the product of the plasmodium, and that the cells are, therefore, the result, rather than the cause, of its formation.

**By Membrane Formation.**—Under this head may be loosely grouped a number of cases in which cytokinesis is accomplished by the formation of membranes more or less independently of mitosis. Such cases are probably not to be sharply set apart from those in which metaplasm, vacuolar material, and mitotic cell-plates are involved. The differentiation of a partition membrane in the cytoplasm between the daughter nuclei after the complete disappearance of the achromatic figure is known in a number of cases, such as the algæ *Stypocaulon* (Strasburger, 1892; W. T. Swingle, 1897) and *Dictyota* (Mottier, 1900). In the cycad embryo the walls separating the cells appear as membranes first in the basal region and gradually differentiate between the nuclei throughout the embryo (Fig. 20). The manner in which the plasmodial endosperm of many angiosperms passes into the cellular condition is very inadequately known. To judge from published figures, it would appear that the partitions delimiting the cells may in different cases arise from centripetal furrows, from membranes independently of nuclear division, and from cell-plates developed in connection with the achromatic figures of the later mitoses. The sporocyte of *Anthoceros*, according to Davis (1899), is divided by membranes after the disappearance of the achromatic figures of the second mitosis.

In the angiosperm embryo sac membranes are formed about the egg, synergids, and antipodal cells, obviously under nuclear influence but often without evident connection with mitosis. Such a development of cells by the differentiation of membranes setting apart portions of the common cytoplasm about free nuclei is often called "free cell-formation." Other examples are seen in the generative cells of some angiosperm pollen grains, the spores of ascomycetes, the egg of *Gnetum*, the proembryo of *Ephedra* (Fig. 87), and the egg of *Pythium* (Fig. 129).

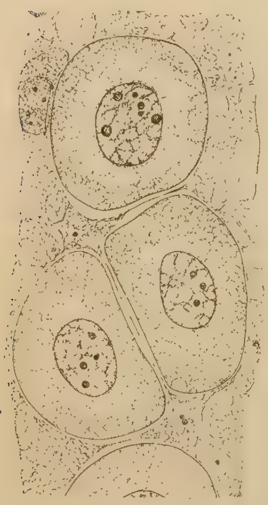


FIG. 87.—Embryonic cells in *Ephedra*, developed by "free cell-formation" in a common mass of protoplasm. (*After Land*, 1907.)

Cytokinesis by the development of membranes, including cases of free cell-formation, is also known in the somatic and reproductive tissues of animals (see Rohde, 1923).

**By Cell-plates.**—Cytokinesis in bryophytes and vascular plants most commonly involves the formation of a *cell-plate* at the equatorial zone of the achromatic figure during the closing phases of mitosis. We have already described (p. 194) the way in which this cell-plate is generally thought to originate—by the fusion of the swollen middle portions of the spindle fibers—and have also pointed out that the actual cell wall is in some way developed in the midst of the cell-plate, apparently between its halves as it splits to form the plasma membranes of the daughter cells (Fig. 88).[1] Although there is some difference of opinion regarding the exact manner in which cell-plates arise, as will be shown, it is clear that in higher plants it is by them, rather than by simple furrowing, that daughter cells in vegetative tissues are usually separated. In many cases cell-plates function in the division of sporocytes also. In the case of sporocytes, permanent walls may develop from cell-plates after both meiotic mitoses, giving bilateral quartets (Allen, 1916, on *Catherinea;* Ekstrand, 1920, on *Isoëtes*), or they may appear only after the second mitosis, giving tetrahedral spores (R. W. Smith, 1900, on *Osmunda;* Devisé, 1922, on *Larix*). In *Nephrodium* (Yamanouchi, 1908) a broad zone of granular protoplasm develops through the equator of the cell after the first mitosis, and after the second mitosis a cell-plate appears in this zone, together with cell-plates in each hemisphere; thus the tetrad is bilateral even though the cell-plates do not appear until after the second mitosis. Such granular zones are chondriosomal (Lewitsky, 1925).

As a result of his investigation of the microsporocytes of *Larix* with fixing reagents not previously used for this purpose, Devisé (1922) has reached a different conclusion regarding the origin of the cell-plate. In *Larix* the cell-plate formed after the first mitosis soon disappears, the division of the sporocyte into tetrahedral spores being brought about by cell-plates formed after the second mitosis. Fibers of spindle substance appear between all four nuclei; but they show no swellings such as Timberlake (1900) reported for *Larix* and other plants, and they take no evident active part in the development of the cell-plates. Each cell-plate first appears as a delicate undulating film in the homogeneous material between the fibers, certain appearances indicating that it actually pushes the fibers together into groups as it becomes straightened (Fig. 78). As the plate substance increases in amount it appears for a time in section as a series of vacuole-like masses separated by groups of fibers. Soon the sides of the plate separate in the region of the fiber groups also, the whole layer coming to be of uniform thickness. The spore cells eventually separate through these fluid layers thus deposited between the four nuclei.

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[1] Strasburger (1898), Timberlake (1900), C. E. Allen (1901).

There are many facts which suggest that the processes of cytokinesis by furrowing, by vacuoles, by membranes, and by cell-plates are not fundamentally distinct from one another, but show a more or less evident relationship (Davis, 1904–1905). The splitting of the cell-plate to form the two new plasma membranes as described by Strasburger and others usually begins at the center and progresses outward, the cleft appearing much like a thin vacuole or series of vacuoles which cut through the cell-plate substance in a manner recalling the behavior of vacuoles in the sporangial cleavages of *Phycomyces.* During cytokinesis in *Larix,* as described above, there are stages appearing like the splitting of a membrane and the fusion of a series of vacuolar masses, and where the separation of the spore cells begins near the periphery the appearance is that of furrowing. Owing to the difficulty of observing such phenomena in living cells, many points must remain in doubt, but it may be helpful to think of cytokinesis by cell-plates in vascular plants as a process whose peculiarities are due not to any fundamental distinctness from the processes commonly observed in thallophytes, but rather to a close association of such processes with the mechanism of karyokinesis.

**The Relation of Cytokinesis to Karyokinesis.**—In the examples of cytokinesis cited in the foregoing pages have been seen all degrees of correlation between cytokinesis and nuclear division. No correlation whatsoever is seen in certain plasmodial masses, cleavage furrows or a series of vacuoles developing through the protoplasm without any evident relation to the nuclei. In other cases the division of the cytoplasm is in some way related to nuclear influence, but not to the mitotic process. Thus cleavage furrows, membranes, vacuoles, or masses of metaplasm may develop in positions clearly dependent upon the positions of the nuclei, the result being definitely uninucleate cells rather than the irregular multinucleate blocks seen in certain cases of plasmodial division. As illustrations may be cited the girdle wall of *Spirogyra* and the subdivision of the endosperm in the cycad. Frequently, as in the budding of yeast and the division of certain sporocytes (*Nicotiana*, *Anthoceros*), the division of the cytoplasm follows so closely upon nuclear division that it seems in some way to depend upon it, without, however, involving the mitotic mechanism itself. Finally, cytokinesis may be so intimately connected with mitosis that the two constitute practically a single process, the presence of the achromatic spindle between the nuclei causing a special series of changes in the plane of cytokinesis. It is to be expected that the resulting "cell-plates" shall differ in certain details, depending on the intimacy of the association of cytokinesis with karyokinesis, and upon the measure in which the achromatic spindle assumes a rôle in the former process. This may be in part responsible for the discrepancies in the accounts of the cell-plate given by various observers. All descriptions based on fixed material are, of course, subject to correction according to the results of any examination of living material which new methods may permit.

## THE CELL WALL

Probably the most striking difference which meets the eye in a comparison of animal and plant tissues lies in the relative degree of distinctness with which the limits of the individual cells may be made out. Animal cells, as a rule, are separated only by very thin membranes, which in many tissues are so delicate as to be scarcely discernible; whereas the cells of plants usually possess conspicuous firm walls, which in the case of woody plants become greatly thickened and afford mechanical support to large bodies.

**The Primary Wall Layer.**—Since the time when cell-division was first carefully studied with the aid of modern methods it has been known that in the cell wall of plants the primary layer, or *middle lamella* (the "intercellular substance" and "cement" of early writers), is formed in most cases in close connection with the achromatic figure at the close of mitosis.[1] The manner of its origin, however, has proved to be a very difficult point to determine, and has formed the subject of a long-continued controversy. During the telophase of mitosis a *cell-plate* in some way differentiates through the equatorial region of the achromatic spindle substance between the daughter nuclei, as pointed out in the foregoing pages. For some time it was thought (Strasburger, 1875, 1882*b*, 1884) that the cell-plate so formed became at once the middle lamella, upon which secondary and frequently tertiary layers were subsequently deposited by the protoplasts on either side. Strasburger here found support for his theory that the cell wall is essentially a transformed layer of the protoplast, in opposition to Nägeli and von Mohl, who regarded it as primarily a secretion product. As a result of further researches, however, he later (1898) abandoned this view and adopted an interpretation that had been suggested by Treub (1878), namely, that the cell-plate soon splits to form the plasma membranes of the two daughter cells, and that there is secreted between these membranes by the protoplasts a substance which becomes the primary layer, or middle lamella.

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[1] Discussion is here largely restricted to the walls in the tissues of vascular plants; the limiting membranes of unicellular organisms have been dealt with in Chapter II. For a complete account of histological differentiations in vascular plants, see Eames and MacDaniels (1925).

Further evidence supporting this view was contributed by Timberlake (1900) and C. E. Allen (1901). Allen was able to show not only that the middle lamella itself may increase in thickness by the addition of new material before the deposition of secondary layers begins, but also that it consists in reality of two layers representing the secretions contributed by the two daughter protoplasts. Where these two masses of secreted material meet there is developed a median plane of weakness which is ordinarily invisible, but along which the lamella invariably splits when intercellular spaces are developed by the rounding up of the cells. By the use of proper staining methods it has been found possible to differentiate this "primary cleavage plane." The continuity of the middle lamella is interrupted, if at all, only by the fine pores through which pass the protoplasmic strands connecting adjacent cells (see p. 66).

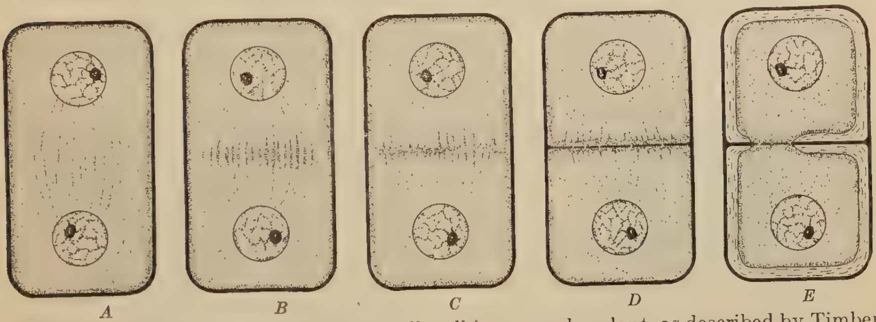

Fig. 88.—The development of the cell wall in a vascular plant, as described by Timberlake and Allen. *A*, telophase of mitosis in meristematic cell. *B*, appearance of swellings on the achromatic fibrils. *C*, fusion of the swellings to form an equatorial cell-plate; fibrils disappearing. *D*, deposition of new primary wall (middle lamella) between the halves of the split cell-plate; the halves of the cell-plate become the plasma membranes of the daughter cells. *E*, deposition of a secondary wall layer between the plasma membrane and the middle lamella, except in the region of a large pit; the closing membrane of the pit has fine perforations. Primary wall drawn in solid black; cytoplasm stippled; plasma membrane densely stippled; secondary wall shaded with lines. (*After Eames and MacDaniels*, 1925.)

**Secondary and Tertiary Wall Layers** (Fig. 88).—It is probable that the deposition of the secondary layer begins after the cell has reached nearly or quite its full size, though to this there are apparently certain exceptions. The secondary layer, which seems to be formed with considerable rapidity, differs from the primary layer not only chemically (see below), but also in structure, being interrupted by circular or elongated areas in which no secondary substance is deposited, so that the cells at these places are separated only by the delicate primary membrane. Such a wall is said to be "pitted," the primary lamella extending across the *pit* being termed the *closing membrane.* The central portion of this membrane sometimes (vascular cells of gymnosperms chiefly) has a more or less conspicuous thickening known as the *torus.* The portion of the membrane around the torus is pierced by fine pores; in some cases these may become so large and numerous that the torus appears to be suspended on a meshwork (Fig. 89), while extreme cases are known in which it is held in place only by a few strands. In *bordered pits* (Fig. 90) the secondary wall overarches the margins of the closing membrane. In this type of pit, characteristic chiefly of water-conducting cells of the gymnosperms, the closing membrane is of such a nature that its position in the center of the pit is readily altered. Probably because of changes in pressure it swings to the side of the pit; the torus then lies against the pit opening, or "mouth," and the pit is blocked except for slow diffusion through the rather thick torus. The latter may even be forced tightly into the pit mouth.

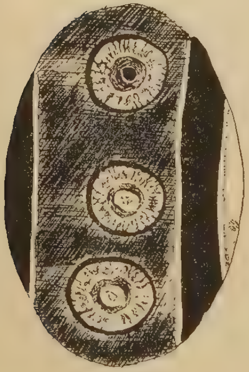

Fig. 89.

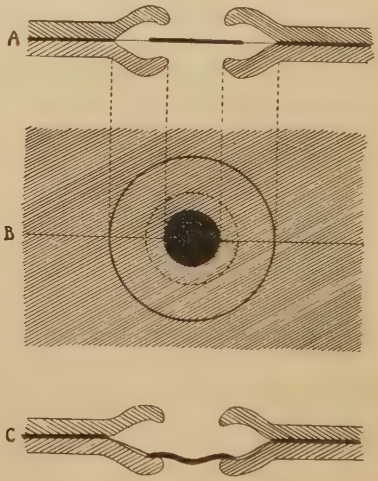

Fig. 90.

Fig. 89.—Pits in the wood of *Larix*, showing lace-like pit membrane. (*After Bailey.*)

Fig. 90.—Diagram of bordered pit in coniferous wood. *A*, section of pit showing closing membrane supporting the torus, and the secondary layer on each side of middle lamella. *B*, face view of the same. *C*, section showing torus forced against mouth of pit. (*After Bailey.*)

The secondary wall layer may be even more limited in extent, only a small portion of the primary wall being covered. Such is the case in protoxylem cells, in which the secondary layer is deposited in the form of rings and spirals (Fig. 13). This form of thickening, together with the peculiarly extensible character of their primary walls, permits the great increase in length of these cells necessitated by the continued growth of the young organs in which they chiefly function. In some cells, notably the tracheids of certain gymnosperms and the vessels of many angiosperms, a tertiary layer is deposited upon the secondary wall. This tertiary layer takes the form of slender spirals, rings, and other figures resembling the secondary thickenings of protoxylem cells.

**The Physical Nature of the Cell Wall.**—Hugo von Mohl (1853, 1858) first expressed the idea that the cell wall grows by *apposition*, *i.e.*, by the deposition of material in successive laminæ. Although certain other workers (Wigand, 1856) supported this view, it became overshadowed for a time by the theory of Nägeli. This investigator, as a result of his classic researches on the wall and on starch grains (1858, 1863, 1864), concluded that the wall is made up of ultra-microscopic crystalline *micellæ* surrounded by water films. Growth of the wall in thickness and in area he believed to be due to the intercalation of new micellæ between the old ones, a process termed *intussusception*. Contrasted with this was Strasburger's development of the apposition theory (1882, 1889). Although Strasburger agreed that the wall had both solid and liquid constituents, he held that the latter were not complex micellæ, but only molecules linked together in the form of a reticular framework by their chemical affinities. Growth in area he thought was merely a matter of stretching without the intercalation of additional particles, while increase in thickness was supposed to be accomplished by apposition, or the deposition of layers of new material in the form of small particles, or "microsomes." The striations which both he and von Mohl observed in the wall substance were regarded by Strasburger as due to the linear arrangement of these particles.

That the cell wall is not merely a lifeless secretion of the protoplast, but contains protoplasm in some form, is a view which has often been upheld, and involves problems which are still far from being solved. Prominence was given to the view by Wiesner (1886), who looked upon the growing cell membrane as a living part of the cell. Following Strasburger's early view, he held the primary layer to be wholly protoplasmic, and supposed the growing wall to be made up of regularly arranged particles, which he called *dermatosomes*, connected by fine fibrils of protoplasm. Growth was accomplished by the intussusception of new dermatosomes. Evidence in support of Wiesner's interpretation was brought forward by Molisch (1888), who showed that when tyloses come in contact pits are formed exactly opposite each other in the two abutting walls, a phenomenon which it would be more difficult to explain were the walls held to be devoid of living substance.

Both the new intussusception theory of Wiesner and the apposition, or lamination, theory of Strasburger had many supporters. According to Pfeffer (1892) both processes, the intussusception of new particles or molecules and the apposition of new material in layers, are concerned in the development of the wall. This view was later adopted by Strasburger (1898), and has received general acceptance. But much work must be done before any final conclusion can be drawn regarding many points. Especially obscure is the exact relationship of the protoplasm and the wall. Hansteen-Cranner (1919, 1922) has recently emphasized anew the conception of the wall as a colloidal network of celluloses and hemi-celluloses, in the meshes of which are extensions of the plasma membrane, this in turn being a colloidal system of lipoids and other materials. This is an important problem whose solution awaits the results of further inquiries by cytologists and biochemists.

**The Chemical Nature of the Cell Wall.**[1]—Through the early researches of a number of investigators[2] it was found that the newly formed cell walls of plants consist chiefly of cellulose and pectic substances. As a general rule, the primary layer seems to be largely pectose, the secondary and tertiary layers being made up of cellulose together with pectose and other materials. It is only rarely, however, that pectose and cellulose exist in anything approaching the pure form. The pectose of the middle lamella soon changes to insoluble pectates, chiefly that of calcium, while the other layers become greatly altered in composition by chemical transformation and the addition of new materials. A certain amount of protein matter seems to be present in all the layers. In the apical meristems of *Vicia faba* Tupper-Carey and Priestley (1923) find the middle lamella to be probably a mixture of pectin and protein, and that the thickened walls, although they all contain cellulose, may not react as cellulose because of the presence of proteins and other substances. The walls in meristematic tissues differ somewhat in composition in root and stem, but in the walls of parenchyma in both apices the middle lamella is composed chiefly of calcium pectate, and the secondary layer mostly of cellulose. The presence of proteins is noteworthy in connection with the question of the relation of the protoplast to the wall.

As the cells become differentiated their walls may undergo chemical alterations of many kinds. One of the commonest changes in xylem cells is due to the appearance of lignin in the secondary and tertiary layers, and the consequent conversion of a part of the cellulose into ligno-cellulose, with its characteristic staining reactions. The transformation is sometimes so complete that ordinary cellulose stains no longer take effect. Ligno-cellulose appears to consist of cellulose and two other substances, one of which seems to be a pentosan. The primary layer occasionally shows some lignification also. Two other substances involved in the transformation of cell walls are suberin and cutin. It is apparent from the investigations of van Wisselingh (1888, 1892, 1895) and Gilson (1890) that these are not distinct chemical substances, but varying mixtures of certain organic acids present in part in the form of fats (Priestley, 1921). They are distinguished more by location than by composition, suberin appearing in the walls of periderm cells (cork), while cutin occurs as a cuticle on the epidermis and often in patches in the walls of subepidermal cells. Lee and Priestley (1924) have ascribed the formation of plant cuticle to certain alterations in fatty substances which are produced in the protoplasts and then migrate into and along the cell walls to the outer surface of the epidermis. The cellulose layer immediately below the cuticle may be impregnated with fat. A variety of mineral substances, such as silica, calcium carbonate, and calcium oxalate, as well as more complex organic compounds, including tannins, oils, and resins, are often deposited in the walls of old cells. The heartwood of trees owes its qualities largely to the presence of these additional materials.

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[1] For general accounts of this subject, see Czapek (1913), Molisch (1913), Gleisberg (1921), Grafe (1911, 1922) and van Wisselingh (1924).

[2] Payen (1842), Frémy (1859), Kabsch (1863*b*), Wiesner (1864, 1886), Mangin (1888–1893), Schulze (1890–1894).

In certain thallophytes the walls are frequently composed largely of chitin, a substance which is more characteristic of animals than of plants. Among the fungi, according to the recent résumé by von Wettstein (1921*a*), chitin or chitin-like substances form the walls of the basidiomycetes, the ascomycetes with the exception of yeasts and Laboulbeniales, and the phycomycetes with the exception of the oömycetes, which have cellulose walls. Although chitin was earlier reported in blue-green algæ, neither D. Wester (1909) nor Mameli (1920) found it in an examination of many species; the walls are here composed rather of cellulose and pectin materials. The membranes of bacteria appear to be mainly pectic in nature. The myxomycetes are sharply distinct from other plant groups in having walls composed of keratin, sometimes with cellulose also, but no chitin. The walls of green algæ in general resemble those of higher plants in composition, but in the vegetative cell walls of a number of species and in zygospores of Zygnemaceæ chitinous layers have been reported by Tiffany (1923) and Wurdack (1923). The walls in red and brown algæ contain peculiar carbohydrates which react like neither cellulose nor chitin.

**The Walls of Spores.**—Various special types of wall-formation are seen in spores, which usually have elaborate walls consisting of two or more layers, or coats. With regard to the spore quartets of bryophytes and vascular plants, one may distinguish two general methods by which such coats are developed, as shown by Strasburger: (1) by the successive formation of layers within the original membrane of the spore cell by the protoplast, and (2) by the deposition of material on the outside of the original membrane by the protoplasmic tapetal fluid in which the young spores lie in the case of many plants.

In the former method the first conspicuous change is ordinarily the development of a more or less temporary gelatinous layer around each of the spore cells, either before or after they have rounded up from one another (Fig. 84). Upon the inner surface of this special layer the protoplast deposits the *exine*, or outer spore coat. In many cases, such as the microspore of *Ipomœa purpurea* (Beer, 1911), this is at first a homogeneous layer that soon differentiates into an outer lamella and an inner zone with net-like thickenings and spines (the "mesospore"). Finally, there is deposited an inner coat, or *intine*. This mode of development is widely prevalent, the walls of most spores showing two principal coats: the exine, which is characteristically thickened and sculptured, and in which, in the case of angiosperm pollen, there are definitely differentiated germ pores through which the pollen tubes later emerge; and the intine, a colloidal pectic layer which, in the seed plants, grows out through the exine as a pollen tube. It is of interest to note that the exine, although it begins to differentiate in contact with the protoplast, may continue to thicken and develop its peculiar markings after it has been separated from the protoplast by other layers (Beer, 1905, 1911; Tischler, 1908). Evidently the building material is secreted by the protoplast, transferred through the intervening colloidal layers, and deposited in the outer coat. The formation of such material in *Lilium croceum* is attributed to chondriosomes by Krjatchenko (1925). According to this author some of the chondriosomes in the microsporocyte enlarge and develop fatty material within them during the course of the meiotic divisions, and later pass to the outer surface of the spore cells, where they become transformed into the system of protruberances arranged in a pattern on the spore coat. Meanwhile the chondriosomes of the tapetal cells form a similar material which is secreted into the anther cavity. In an extensive study of the composition of pollen-grain walls Biourge (1892) showed that they contain cutin, callose, cellulose, and pectic substances, singly or in various combinations.

The highly specialized coats of the megaspore of *Selaginella* have been carefully studied by several workers. In *S. rupestris*, according to Lyon (1905), whose account differs from those of Fitting (1900, 1906) with regard to certain points, each spore becomes surrounded by a thick gelatinous membrane at the close of the sporocyte divisions. In the midst of this gelatinous layer the spore coats begin to differentiate. The *exospore* first appears as a double zone, the outer part of which becomes the *perinium* (Fig. 91). The small protoplast now expands and pushes outward the undifferentiated inner portion of the gelatinous layer, and as it does so a second coat, the *endospore*, is formed at its surface. In *S. emiliana* the exospore and endospore develop simultaneously. Lyon thus finds two coats in place of the three reported by Fitting, but points out that a portion of the gelatinous layer may remain in an undifferentiated condition until a late stage and thus appear like an intermediate coat. The exospore and endospore evidently correspond to the exine and intine of other spores.

It remains to describe the other general method of spore coat formation, whereby one or more layers are deposited on the outside of the spore by a tapetal fluid in which the young spores lie. In vascular plants the sporangium (the anther in the case of the angiosperms) is lined by a layer of special nutritive cells known as the *tapetum.* In many known cases, including *Equisetum, Botrychium, Marsilia,* and a number of angiosperms, the boundaries of these cells break down, allowing the protoplasts to coalesce and form a "tapetal plasmodium," or "periplasmodium," which flows in among the immature spores and contributes to the development of their coats (Fig. 92). In *Equisetum,* according to Beer (1909*b*) and Hannig (1911), the spore has three coats: an *endospore,* an *exospore,* and a *perispore,* the last-named being formed by the plasmodium and consisting of several layers. At first the young spore cell has a simple membrane. Upon this membrane the plasmodium deposits successively an inner gelatinous layer, a second layer, an outer gelatinous layer, and finally a layer which later splits up to form the characteristic appendages of the spore. These four layers together constitute the perispore. While they are in the process of formation the original spore membrane becomes transformed into the exospore, and within it the endospore is developed last of all.

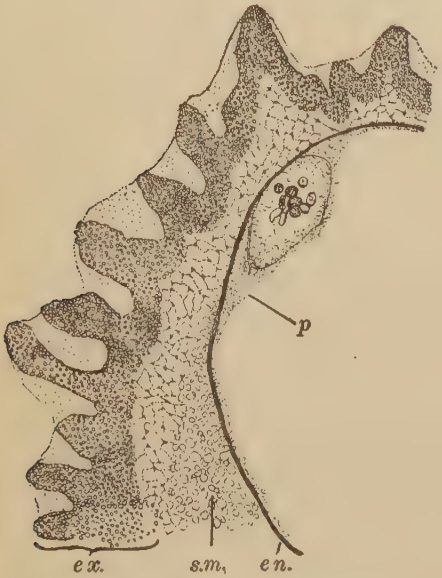

FIG. 91.—The developing megaspore coat of *Selaginella rupestris.* *p,* protoplast with nucleus; *en,* endospore; *s.m.,* undifferentiated portion of gelatinous layer; *ex,* exospore; the denser portion is the "perinium." (*After Lyon,* 1905.)

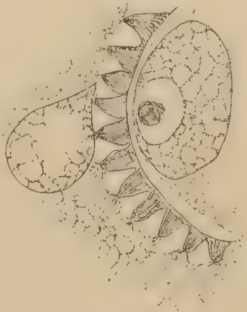

FIG. 92.—The exine of the microspore (right) developing in contact with the tapetal plasmodium (left) in *Commelina cœlestris.* (*After Tischler,* 1915.)

The formation of the peculiar walls of spores is thus seen to involve a special protoplasmic activity, protoplasm of cells other than the spores often sharing in the process. Cytological interest at present centers chiefly in other matters, but further studies on spore coats might contribute much toward the solution of the important problem of the possible existence of protoplasm in cell walls.

**The Intercellular Substance of Animals.**—The problem of the relation of the protoplasm to partitions which subdivide it into cells is encountered in animals as well as in plants. Zoölogists have differed widely in their interpretations of the "intercellular substance" composing such membranes in animal tissues. Heidenhain (1902, 1907) emphasized the view that this substance is metaplasm, a special form of living substance which differentiates in protoplasm in connection with special functions, and which is capable of growth, response to certain stimuli, and further differentiation. This is also the view of Rohde (1908, 1914, 1923) (see p. 47). A. Meyer (1896, 1920) is strongly opposed to this conception, holding that the albuminous intercellular substance of animals, like the carbohydrate wall of plants, is ergastic in nature, and not to be classed with metaplasmic (alloplasmatic: Meyer) differentiations. The fibrils frequently observed in the intercellular substance, which many have taken as indications of its metaplasmic nature, Meyer regards as modifications of the ergastic material, or as substances which have arisen in protoplasmic connections.

The membranes of animal cells differ from those of most plants in consisting largely of such substances as chitin, elastin, keratin, and gelatin, rather than cellulose and related carbohydrates. Cellulose has been found only rarely among animals. In the ascidians, as has long been known, the outer layer of the body wall consists largely of cellulose; and a cellulose-like substance has recently been found in the skeletal plates of an infusorian (Dogiel, 1923*a*).

**Conclusion.**—In concluding this discussion of the means by which protoplasm is subdivided attention may again be directed to what was stated at the end of Chapter III regarding the significance of this subdivision. The subdivision of sporocytes and other reproductive cells obviously has its chief biological meaning in the free state of the spores or gametes which are thus formed. In somatic tissues whose cells remain in continuity the partitioned condition allows a fuller play to forces acting at surfaces and in thin films, and a more perfect specialization of functionally distinct regions, and so has unquestionably played a highly important rôle in the evolution of organisms.

## CHAPTER XII

# AMITOSIS, ATYPICAL MITOSIS, AND OTHER NUCLEAR PHENOMENA

In the foregoing discussions of nuclear division only typical mitosis as it occurs in the great majority of plant and animal tissues has been considered. It remains to review briefly certain additional modes of division and other phenomena which may be of minor importance, but which will serve to broaden our conceptions of the nucleus and its behavior.[1]

**Amitosis.**—In amitotic or direct nuclear division the nucleus simply constricts and separates into two portions while in the metabolic, or "resting," condition, no condensed chromosomes or achromatic figure being formed. Sometimes the portions are very irregular in size or more than two in number; such cases are often referred to as nuclear budding and "fragmentation" (Tischler, 1901). Such nuclear divisions are usually not followed by cytokinesis, the cells thus coming to have two or more nuclei. Amitosis was at one time looked upon as the normal mode of nuclear division, mitosis being somewhat exceptional, but the true state of affairs, so far as higher organisms are concerned, has turned out to be quite the reverse, mitosis occurring almost universally and true amitosis in comparatively few well-authenticated cases. It seems that binucleate cells, constricted or irregularly lobed nuclei, and a number of other appearances have in the past been freely taken as evidences of amitosis, whereas it is now known that such conditions may represent the results of deranged mitoses or nuclear fusions. It is in the light of this possibility that one should interpret a large number of reported instances of amitosis. Among the lower organisms amitosis appears to be of rather frequent occurrence. Some of them show both mitosis and amitosis. In certain yeasts (*Saccharomyces cerevisiæ*) amitosis occurs at the time of budding and mitosis at spore formation (Guilliermond, 1912*b*, 1920). Certain other species show a simple form of mitosis in the vegetative divisions (Janssens and Leblanc, 1898).

The occurrence of amitotic phenomena in cells with a distinctly nutritive function, such as tapetal, antipodal, and endosperm cells of angiosperms and certain gland cells of animals, lends support to the hypothesis of Chun (1890) that amitosis aids in the process of metabolism by increasing the nuclear surface. That the phenomena in tapetum are truly amitotic has been questioned (Bonnet, 1912, and others), but Tischler (1921–1922) thinks it probable that amitosis as well as deranged mitosis and nuclear fusion may occur in tapetal cells and periplasmodia.

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[1] For a review of the literature pertaining to amitosis and irregular mitosis in plants, see Tischler (1921–1922, Chap. 7). For the literature on amitosis in animals, see Conklin (1917) and Nakahara (1918*b*).

Another very prevalent opinion regarding the significance of amitosis is that expressed by Flemming (1891), namely, that the process is primarily a degenerative phenomenon, since it is so frequently observed in pathological tissues. In the words of vom Rath (1891), "when once a cell [nucleus] has undergone amitotic division it may indeed continue to divide for a time by amitosis, but inevitably perishes in the end." That this interpretation cannot be of universal application has been contended by those who have found amitosis, or amitosis-like appearances, in cells which show no visible sign of degeneration.[1] It is of interest in this connection to note that the few observed cases of amitosis in living tissues have occurred mostly in cultures which were becoming old. Nuclear fragmentation and budding occur frequently in cells which show distinct signs of degeneration (see Lewis and Lewis, 1924). It is the opinion of Kofoid (1923) that the supposed amitosis in Protozoa is a degenerative or pathological phenomenon, or in some cases a special form of mitosis which has been incorrectly interpreted. Although it has been held that a nucleus which has undergone amitosis may subsequently divide mitotically, Agar (1920) states that no real proof exists for this. Such is also the opinion of Schürhoff (1919*a*) and Sakamura (1920). Chambers (1917) has shown, however, that mitosis may follow the reunion of the parts of a nucleus artificially pinched in two.

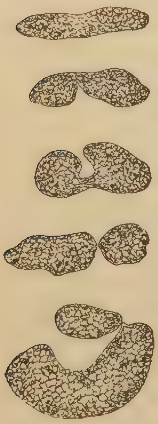

Fig. 93.—Amitosis in internode of *Chara*.

Aberrations of the mitotic process such as those which occur in abnormal tissue, and which have so often been mistaken for amitosis, may be produced artificially by a variety of means. The effects of chloral hydrate, ether, and other anesthetizing agents have been studied by several investigators.[2] In root tips and other plant tissues subjected to the influence of these reagents the normal course of mitosis is disturbed in various degrees, depending on the strength of the dose. Characteristically the achromatic figure develops poorly or not at all, and the chromosomes scatter irregularly in the cell. They may form one or more groups and reorganize nuclei which are often connected by bridges (Fig. 94). Fusions of nuclei so produced frequently occur. Thus it is not uncommon to find all gradations between normal mitosis and what looks like amitosis, and certain observers (Pfeffer, Nathansohn) concluded that periods of true amitosis might be induced by treating *Spirogyra* filaments with ether. Many have adopted the view that the two forms of division are not fundamentally distinct, both occurring without impairing development. This view has been opposed by Haecker (1900) and more recently by Sakamura (1920), whose experiments have shown that such "induced amitosis" and the "transitional states between mitosis and amitosis" are all to be interpreted as derangements of the mitotic process. True amitosis is held to be something quite distinct from these phenomena; hence Haecker terms the latter "pseudoamitosis."

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[1] Des Cilleuls (1914) on rabbit cells; Saguchi (1917) and Helvestine (1921) on ciliated cells of vertebrates and invertebrates; Bast (1921) on bone; Kisser (1922) and others on vegetative tissues of plants; F. E. V. Smith (1923) on *Saprolegnia*. That the frequent reports of amitosis in the pith and cortex of angiosperms have been due to misinterpretations has been shown by Beer and Arber (1919) and Schürhoff (1920).

[2] Pfeffer (1899), Nathansohn (1900*a*), Němec (1904, 1910*a*), Sakamura (1920), van Regemorter (1925).

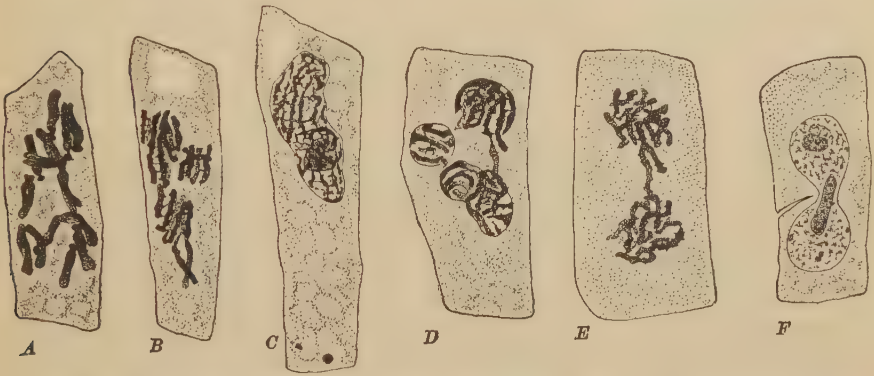

FIG. 94.—Abnormal mitosis in chloralized root cells of *Vicia*. *A*, irregular distribution of chromosomes. *B*, scattered chromosomes beginning to assume nuclear form. *C*, nucleus reconstructed by scattered chromosomes. *D*, chromosomes reconstructing three separate nuclei instead of one. *E*, chromosomes reconstructing two nuclei connected by a bridge. *F*, amitosis-like appearance resulting from condition shown in *E*. (*After Sakamura*, 1920.)

Similar aberrations may result from treatment with Röntgen rays, as has been shown by Komuro (1917, 1922, 1924) for the root tips of *Vicia faba* and by Alberti and Politzer (1923, 1924) for cornea cells of urodele larvæ (Fig. 95). Not only do mitotic aberrations lead to amitosis-like appearances similar to those in chloralized cells, but to a variety of other degenerative phenomena involving particularly the nucleus.[1] The cytological resemblance of these cells to those of tumors is very striking, and is of interest in connection with the questions of the nature and treatment of such growths.[1]

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[1] Chromatic matter of the nucleus contracted into a deeply staining homogeneous mass (pyknosis), or dissolved in the karyolymph (karyolysis), or adherent to the nuclear membrane; disorganization of the nuclear membrane; escape of nucleolar matter into the cytoplasm, etc.

Aberrations of mitosis have also been caused experimentally by ultra-violet rays (Takamine, 1923; Schleip, 1923), radium (Mohr, 1919; M. Williams, 1925), and low temperature (Mohr; Borgenstam, 1922).

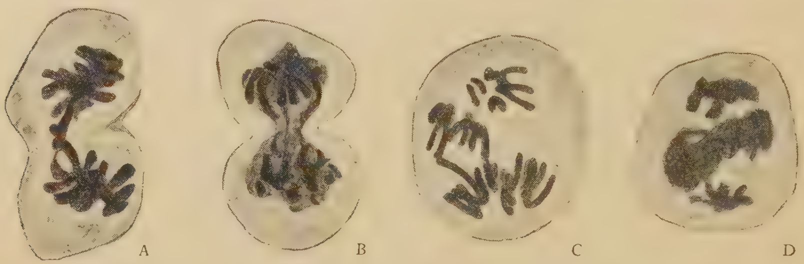

FIG. 95.—The effect of Röntgen rays on mitosis in cornea cells of *Salamandra*. *A*, chromatic bridge. *B*, "pseudoamitosis." *C*, distribution of chromosomes to three centers. *D*, partial pyknosis; some of the chromosomes have passed to the poles. (*After Alberti and Politzer*, 1923.)

*Amitosis and Heredity.*—One of the most important theoretical questions raised by the phenomenon of amitosis is that of the effect which the process may have upon the hereditary mechanism. According to the chromosome theory of heredity and development in its usual form, it has been thought that, although amitosis may occur in connection with an altered metabolism in tissues not to undergo further differentiation, mitosis must occur exclusively in the germ cell lineage, in order that the chromosomes and the hereditary elements they contain shall be properly distributed to the reproductive cells; and also in developing tissues and organs, so that differentiation may proceed normally. The hereditary mechanism, as will be shown in later chapters, is supposed to be of such a nature that amitosis would seriously derange its organization, each daughter nucleus of such a division lacking some of the elements necessary for normal functional activity because of the simple mass division of the nuclear substance. A considerable number of investigators have contended, however, that amitosis may occur in the course of normal cell differentiation, and that this constitutes evidence against the chromosome theory of heredity.

This question has been closely examined by Conklin (1917) in connection with his investigation of maturation and cleavage in *Crepidula plana*. In this form it is found that there are many apparent cases of amitosis, but careful observations show that they are all modifications of the mitotic process. Thus chromosomes may scatter and fail to unite in a single nucleus; mitosis may occur without cytokinesis, giving cells with two or more nuclei; certain chromosomes may fail to separate in the anaphase, leaving a bridge between the daughter nuclei; the nuclear membrane may persist throughout mitosis and finally divide by constriction. Any of these aberrations may give rise to the conditions interpreted as amitosis. As a result of his many observations and an examination of the evidence offered by others, Conklin concludes that there is not a single conclusive case of true amitosis in normally differentiating cells, and that all attacks upon the chromosome theory on the ground of amitosis have signally failed. The phenomena observed by Sakamura (1920) in chloralized plant cells are strikingly similar to those seen by Conklin in *Crepidula*, and his conclusions regarding the chromosome theory are essentially the same.

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[1] Howard and Schultz (1910), Boveri (1914*a*), Bichler (1914), Yamagiwa and Ichikawa (1915–1919), Komuro (1924*d*, 1925).

It is evident that the problem of the effect of amitosis on the differentiation of the tissues in which it occurs and on the hereditary powers of the nucleus is more difficult to solve than some have supposed, and that much caution is necessary in interpreting amitotic appearances in fixed preparations. Investigations on deranged mitosis have shown that many of the reports of amitosis in normally differentiating tissues were clearly due to misinterpretation, and have laid many more of them open to question. It has not yet been shown with certainty in any case that the descendants of nuclei said to divide amitotically in young germ cells ever become the nuclei of normal gametes. It has been suggested that a nucleus resulting from amitosis may regenerate the lost parts, but it is known that chromosomes lost in abnormal mitotic division are not regenerated. Should it be proved, however, that one portion of an amitotically divided nucleus functions as the original whole in development and heredity, a serious obstacle would be placed in the way of the chromosome theory in its current form.

**The Cyanophyceæ.**—The structure of the cell in the blue-green algæ has long been a subject of controversy. The chief question at issue has been the nature of the central region, which appears relatively colorless and rather indefinitely limited in living material.[1] Cytologists have differed widely in their opinions of this "central body." Some have denied its nuclear nature, but the more general opinion has been that it corresponds to a nucleus; and some have described a process more or less closely resembling the mitosis of other plants (Hegler, Kohl, Olive, W. H. Brown). Although much of the disagreement is undoubtedly to be attributed to differences in fixation and interpretation, it is also true that different species show a considerable diversity of cell organization, the central region being rather sharply delimited from the peripheral portion in some species, but not at all so in others (Gardner, Guilliermond, Acton).

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[1] The principal cytological works on the Cyanophyceæ are those of Bütschli (1896), Fischer (1897, 1905), Hegler (1901), Kohl (1904), Olive (1904), Phillips (1904), Gardner (1906), Guilliermond (1906), W. H. Brown (1911*a*), Acton (1914), Baumgärtel (1920), and Haupt (1923). Convenient résumés are given by Olive and Haupt. Lloyd (1924) has given special attention to the pigments. The subject of nuclear phenomena in lower plant groups is reviewed by Pavillard (1910).

Guilliermond (1906) observed a number of degrees of concentration of the chromatic material of the cell in the species he examined. In *Scytonema cincinnatum* this material, though forming a sort of reticulum, extends throughout the protoplast, no "central body" being present. In *Phormidium*, *Nostoc*, and *Rivularia* it tends to be more concentrated in a central mass, which in some cases has much of the character of a true nucleus, with nucleolus-like inclusions. In all cases the reticulate mass is divided by an amitosis-like process. Gardner (1906) also observed that the central "nuclear" region showed various degrees of delimitation from the peripheral portion of the protoplast; in only one of the species examined, *Synochocystis aquatilis*, did he find anything approaching mitotic behavior.

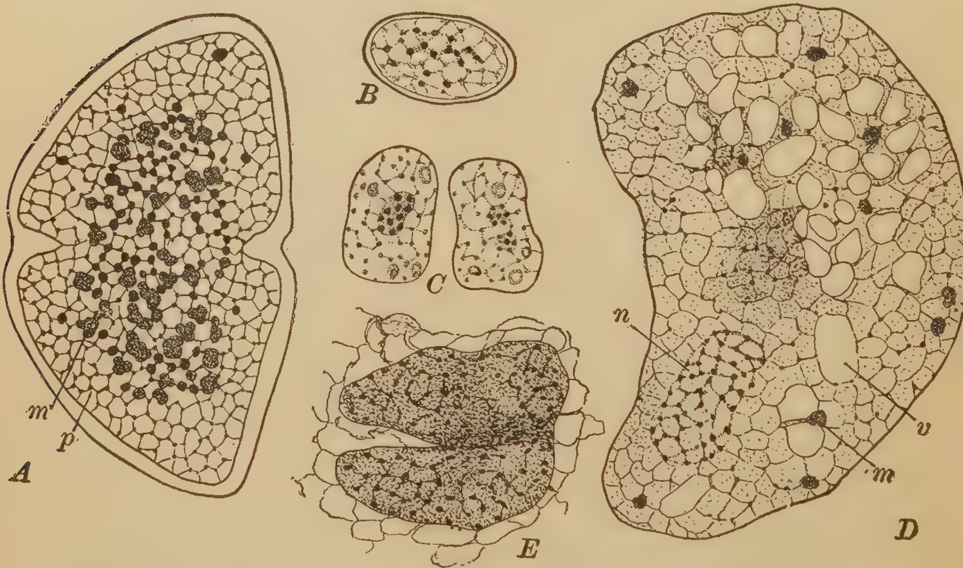

FIG. 96.—The nuclei of various members of the Chroococcaceæ. *A*, *Chroococcus turgidus*, with scattered metachromatin granules (*m*) and plasmatic microsomes (*p*); division beginning. *B*, *Glœocapsa*, with chromatic granules. *C*, *Merismopedia elegans*, showing two stages of nuclear division. *D*, *Chroococcus macrococcus*: *n*, nucleus; *m*, metachromatin; *v*, vacuole. *E*, dividing nucleus of *Chroococcus macrococcus*. (*After Acton*, 1914.)

A particularly interesting series has been described by Acton (1914) for members of the Chroococcaceæ (Fig. 96). In *Chroococcus turgidus* the protoplast is made up of a ground substance with a reticulum bearing bodies of two sorts: granules of *metachromatin* closely similar to karyotin in reaction, and *cyanophycin granules*, or "plasmatic microsomes." Although there is no definitely delimited central region in the cell, the metachromatin is found mostly at the center and the cyanophycin mostly nearer the periphery. When the metachromatin granules become numerous, division sets in, a centripetally growing wall cleaving the protoplast into two daughter cells. In *Glœocapsa* the central region is somewhat more definite and may often show a spireme-like appearance, but this may possibly be an artifact. In *Merismopedia elegans* there is a definitely delimited nucleus, not like that of the higher plants, but merely an accumulation of the chromatic material which divides just before the cell constricts into two portions. In *Chroococcus macrococcus*, finally, the nucleus and cytoplasm are sharply distinct, the former having a reticulum with chromatic granules at its nodes, and dividing by a sort of constriction at the time of cell-division. The arrangement of the chromatic matter reported for *Glœocapsa* is found also by Haupt (1923) in both this genus and *Anabæna* (Fig. 97, *C-I*), but this investigator insists that the protoplasmic ground substance is alveolar rather than reticular.

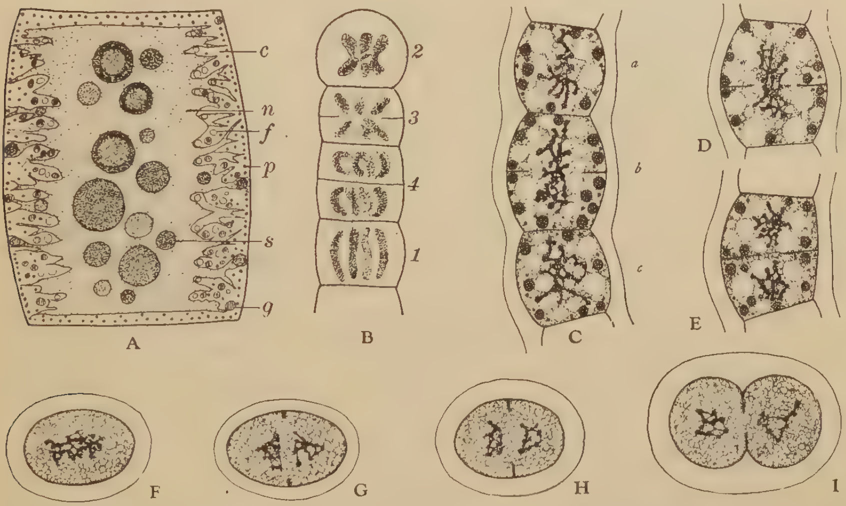

FIG. 97.—*A*, *B*, the structure and division of the cell of *Tolypothrix lanata*, according to Kohl (1903). *c*, cytoplasm; *n*, nucleus; *f*, fat droplets; *p*, phycocyanin and chlorophyll granules; *s*, slime globules; *g*, cyanophycin granules. *C–E*, *Anabæna circinalis*, showing stages in division. *F–I*, four stages in the division of *Glœocapsa æruginosa*. (*C–I after Haupt*, 1923.)

The closest approaches to the nuclear conditions of higher plants are those reported by Olive (1904) for *Oscillatoria* and Brown (1911) for *Lyngbya*. Olive described an achromatic spireme with chromatic masses, which he regarded as chromosomes, and fibrous differentiations resembling a spindle (Fig. 98). The vegetative cells were found almost constantly in division, but in the heterocyst a distinct nucleus with a membrane appeared before the degeneration of the cell. Brown also observed a rather distinct nucleus and spindle-like appearances. Kohl (1904) described a peculiar form of chromosome division in *Tolypothrix* (Fig. 97, *A*, *B*). These observations are very suggestive, but it will not be possible to place the proper evaluation upon them until more such studies have been made with a wider range of fixation methods. In the cases described by most observers the division of the nucleus appears to be at best a form of amitosis, without adequate evidence for the existence of autonomous chromosomes.

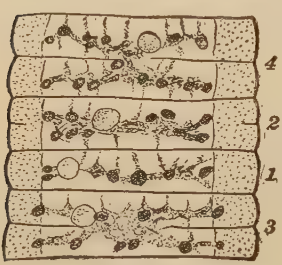

Fig. 98.—Four stages in division in *Oscillatoria Frœlichia*. (*After Olive*, 1904.)

Cytokinesis in the blue-green algæ is generally brought about by the formation of a ring-like wall which grows in from the lateral wall (Figs. 97, 98). The new wall may begin to develop either before or after the division of the central chromatic mass has been completed. As a rule there is no visible evidence of the dependence of wall-formation on the chromatic mass, though in *Lyngbya* Brown reports that the "spindle" seems to be involved. The rounding up of the cells during the late stages of division may give the appearance of constriction.

The peripheral portion of those blue-green alga cells having a fairly well-delimited central "nucleus" has been regarded as cytoplasm by practically all investigators; thus the different species have been thought to show various degrees of differentiation of the protoplasm into these two regions. The manner in which the pigments are held within the peripheral protoplasm, however, has been a much debated question. It was the peculiar view of A. Fischer (1897, 1905) that this peripheral region represents a single large chromatophore, the central region being not nuclear, but the principal mass of cytoplasm, in which a special reserve carbohydrate, "anabænin," accumulates, to be distributed by "pseudomitosis" when the cell divides. Although a pigment-containing mass of protoplasm is in a sense a chromatophore, other workers have opposed such a homology between the peripheral region as a whole and the plastids of other plants, holding rather to the more plausible view that this region is simply protoplasm showing no differentiation of special pigmented organs. The general opinion of students of the group at present is that the pigments are diffused more or less uniformly through the peripheral protoplasm, probably in the form of minute vacuoles which may show a tendency to collect at certain regions, and which have been mistaken for plastids ("cyanoplasts"). It is by no means certain, however, that all the pigments which occur in these plants are borne in the same way, and many points require further investigation (see Lloyd, 1924).

Other inclusions conspicuous in the cells of many blue-green algæ are the "cyanophycin granules" of the peripheral region and the "slime globules" of the central region. These characteristic but more or less transitory bodies seem to represent reserve food substances, probably of an albuminous nature, and show great variation in size and abundance under different nutritive conditions.

It is tempting to search among lowly organized plants and animals for simple modes of nuclear behavior which will shed light upon the origin and significance of the elaborate karyokinetic process so universally found in the cells of higher animals and plants. It is to be acknowledged that such a phylogenetic explanation of mitosis is very far from being reached, but many of the observations recorded are nevertheless of a very suggestive nature. Although the Cyanophyceæ probably had nothing directly to do with the evolution of higher plants, one sees within the group a series of stages such as may well have occurred in the evolution of the nucleus and its complicated mitotic division. In the simplest forms the material concerned with those activities which in higher organisms are associated with the nucleus is scattered throughout the cell without the morphological distinctness characteristic of an organ in the strict sense. It is passively distributed to the daughter cells when the cleavage wall is formed at the time of cell-division. In other cases this material reacts more strongly like true karyotin, and may form a more or less definite aggregation separating into two masses as the cell divides. Finally, definite and well-organized nuclei are present in certain species described in the foregoing pages; and although these nuclei may lack some of the features exhibited by the nuclei of higher organisms, they show in the division and distribution of their chromatic elements many hints of mitosis. The possibility of the evolution of the nucleus-and-cytoplasm type of organization through such a series of stages has been emphasized by Acton and by students of other groups of organisms. The Cyanophyceæ afford an illustration of "the conception of cell structure which implies differentiated regions of a colloidal system in which special processes have become localized and tend to remain fixed" (Harper, 1919).

**The Karyosome Nuclei of Protista.**—The nuclei of many Protozoa and flagellates are characterized by the presence of a large, deeply staining central body known as the *karyosome*. It may appear like an ordinary nucleolus in which all or part of the chromatic material has been stored, but its remarkable centrosome-like behavior at the time of mitosis and its relation to other organs of the cell have shown that it is much more than this.[1] Ordinarily, it elongates and divides at the time of mitosis (Fig. 99), often appearing like a combined nucleolus and centrosome. In some cases the centrosomal element seems to be more distinct from the other nuclear constituents, which has led to certain speculations concerning the origin of the centrosome of Metazoa. In certain flagellates the blepharoplast, or flagellum-bearing organ (Fig. 152), evidently arises from the karyosome, with which it may remain connected by a chromatic strand or rhizoplast. The neuromotor system involves these and often other elements. Such differentiations occur in great variety in different Protista, and have long been very imperfectly understood. Recent investigations, particularly those of Kofoid and his associates, have cleared up many points, and promise to lead to much truer conceptions of this remarkable series of protoplasmic differentiations.[1]

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[1] In the literature it is variously termed the *karyosome* (Hartmann), *endosome* (Minchin), *nucleo-centrosome* (Keuten), and *Binnenkörper* (Doflein, Tschenzoff). With regard to the use of the term "karyosome" in another sense, see p. 89. For general accounts of the nuclei of Protista, see the works of M. Hartmann (1911), Minchin (1912), and Doflein (1916).

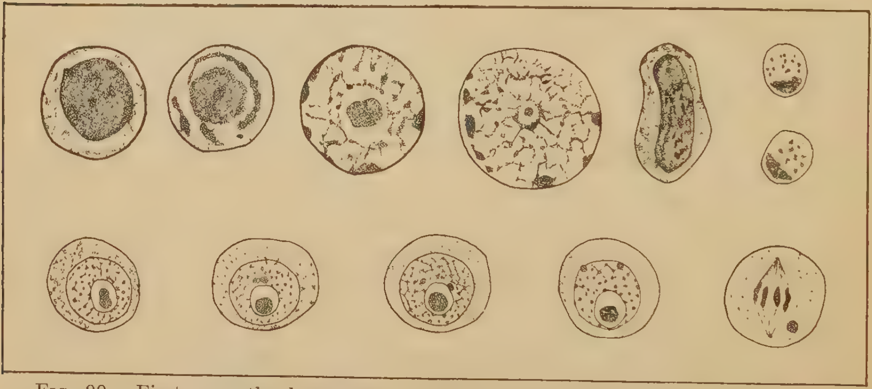

Fig. 99.—First row: the karyosome nucleus of *Entamœba tetragena*, showing cyclic changes undergone by the karyosome, and two stages of "karyosome promitosis." (*After M. Hartmann*, 1908.) Second row: *Myxobolus pfeifferi*, showing origin of centriole from karyosome, and mitosis. (*After Keysselitz*, 1908.)

With regard to the behavior of the chromatic nuclear material in such nuclei, it has been found in those cases which have been adequately studied that chromosomes are formed in the nucleus and divide as in other organisms, but the presence of the dividing karyosome and the persistence of the nuclear membrane give the mitotic figure a peculiar aspect. In *Euglena* the elongated chromosomes, after lying parallel to the dividing karyosome, become less regularly grouped at the equator of the nucleus, where their halves begin to separate and move toward opposite ends of the karyosome. The nuclear membrane remains intact throughout mitosis, and finally constricts at the equator after the division of the karyosome and chromosomes is completed. In the early account of Keuten (1895) the mode of chromosome division was not made evident, but Tschenzoff (1916) and Tannreuther (1923) state that a longitudinal splitting occurs during the anaphase or telophase. Hall (1923) is unable to confirm this in *Menoidium*. Other somewhat similar cases are illustrated in Fig. 100.

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[1] See the papers of Kofoid and Christiansen (1915), Kofoid and Swezy (1915–1922), Hall (1923), Wenrich (1921), Boeck (1917), Swezy (1915, 1916, 1922).

As critical researches on the Protista multiply it becomes increasingly evident that many of these organisms are in all essential features like higher forms in their chromosomal mechanism. Both Metcalf (1915) and Kofoid (1915, 1923) have emphasized this fundamental similarity of protozoan and metazoan nuclei. In some representatives of all the main groups of Protozoa, elongated chromosomes, which split and show evidence of being made up like those of Metazoa, have been found. In certain flagellates Kofoid states that the chromosomes are constant in number and differ in size and shape. The inference is that these organisms possess the same type of Mendelian mechanism as is found in other groups. There are genetic data which indicate that, so far as their life cycles show agreement, Protozoa and Metazoa exhibit similar modes of inheritance (see Jennings, 1920). In many Protista, on the contrary, this high degree of nuclear differentiation seems not to have been reached.

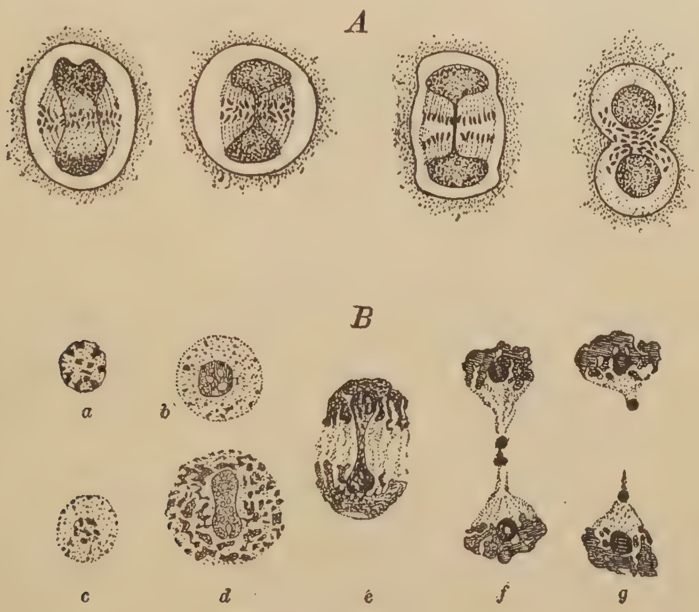

Fig. 100.—*A*, one form of mitosis in *Amœba diplomitotica*. (*After Aragao.*) *B*, nuclear division in *Coccidium schubergi*. (*After Schaudinn.*)

In connection with the possible relation of karyosome nuclei to nuclei of the ordinary type, such cases as that of the green alga *Cladophora glomerata*, as described by T'Serclaes (1922), are of considerable interest

(Fig. 101). In this species the essential features of chromosome behavior are the same as in higher plants, the nuclear reticulum resolving itself into slender chromosomes which shorten, split longitudinally, pass to the poles, and reorganize daughter nuclei. Since no achromatic figure in the ordinary sense is differentiated, the chromosomes do not all separate at once; this, together with the persistence of the nuclear membrane throughout mitosis, and especially the behavior of the nucleolus, results in a series of stages closely resembling those exhibited by typical karyosome nuclei. Although certain smaller nucleoli disappear early, the principal nucleolar mass stretches out and breaks at the middle into two portions associated with the two chromosome groups. Often the breaking is more irregular, nucleolar fragments being left between the two new nuclei, where they are later resorbed. The elongated nuclear cavity becomes dumb-bell-shaped, but just how the cavities of the daughter

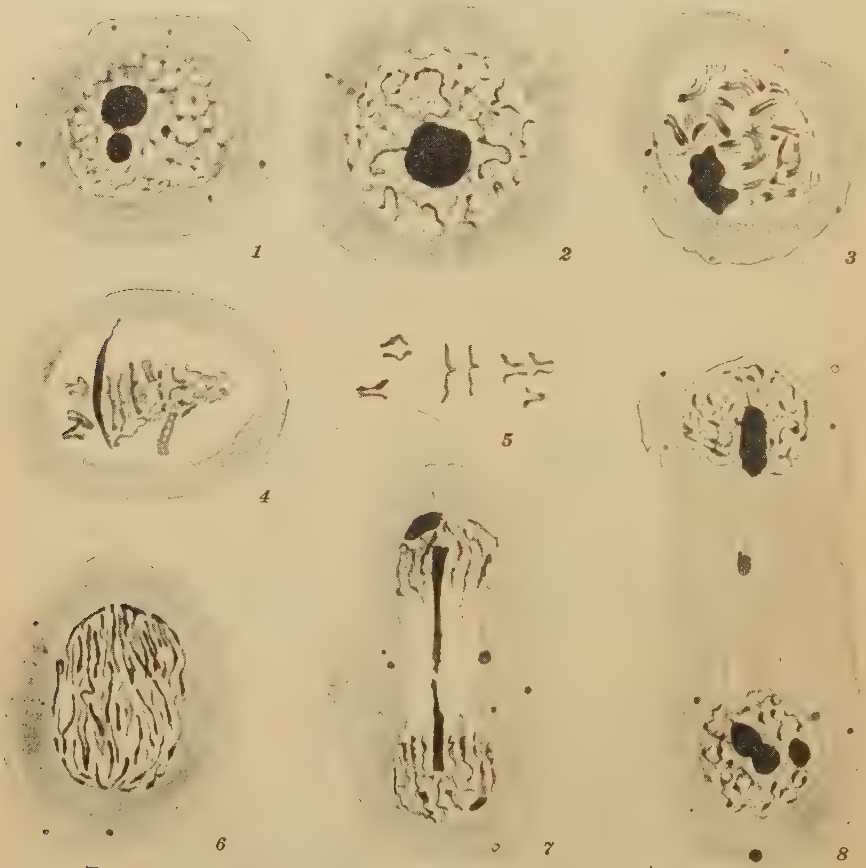

Fig. 101.—Mitosis in *Cladophora glomerata*. (*After T'Serclaes*, 1922.)

nuclei are finally completed is uncertain. It is possible that the tubular connecting portion may sometimes constrict as other authors have stated, but often the connection, with nucleolar fragments in it, is still visible after the cavities of the daughter nuclei are almost completely closed in. Němec (1910) also has described such a nucleolar behavior in the same species, but in the variety *simplicior* and in the related *Rhizoclonium heiroglyphicum* Carter (1919*c*) reports that the nucleoli disappear in the early prophase, as in mitosis in most higher plants.

Such facts suggest that karyosome nuclei and the nuclei of higher plants differ chiefly in the degree of association of chromosomal and nucleolar elements, and that as this association is maintained for shorter and shorter periods the nucleolus becomes less conspicuous and less permanent throughout the nuclear cycle. This is further suggested by other algæ showing an intimate association of the chromosomes and the nucleolus, as well as by the behavior of the nucleolus in mitosis in higher plants (pp. 90, 159). Conditions intermediate between the karyosome nucleus, which involves a centrosomal element, and the condition in higher animals, in which this element is wholly distinct, are also known. Chromosomal, centrosomal, and nucleolar protoplasmic constituents are combined in the karyosome of lower organisms, and variously separated in higher animals and plants; but phylogenetic speculations based on these phenomena are at present more tempting than profitable.

**Chromidial Substance.**—The term *chromidia* is usually understood to mean small granules, strands, or irregular masses of "chromatin" not aggregated into a definite nucleus; it includes the scattered chromatic material of Protista having no formed nuclei, as well as such material in the cytoplasm of nucleated cells. No end of confusion, however, has arisen from the lack of a specific stain for chromatin; a number of protoplasmic inclusions which are certainly not chromatin have been called chromidia by different observers. As Cowdry (1924) says:

> . . . in practice, under the heading of chromidia, we have therefore to deal with a variety of substances which have been hastily grouped together on account of their general affinity for "basic" stains and their supposed relation to nuclear chromatin and for which no special methods of fixation are required. It is a branch of cytology which has developed almost wholly apart from methods for the study of living cells.[1]

R. Hertwig (1902, 1904) described what appeared to be an emission of chromatic granules from the nucleus into the cytoplasm in a protozoan, *Actinosphærium Eichorni*. As a result of this and other observations he formulated the "chromidial hypothesis," which received the support of certain other biologists (*e.g.*, Goldschmidt, 1904, 1910) and became the subject of a long controversy. According to this hypothesis, there are in the nucleus two kinds of chromatin: "idiochromatin," concerned in reproduction and heredity, and "trophochromatin," or "somatochromatin," concerned in nutrition. The chromidia are granules of trophochromatin derived from the idiochromatin and transferred to the cytoplasm; this is a self-regulatory process by which the proper nucleoplasmic ratio, which Hertwig regarded as of much importance, is maintained. Hertwig stated that the chromidia degenerate into a brown pigment, but Goldschmidt and others laid emphasis on their apparent rôle in growth and the differentiation of special functional cell structures. It was further suggested (Schaudinn, 1903; Goldschmidt, 1904, 1910) that in the infusoria the micronucleus contains the idiochromatin and the meganucleus the trophochromatin, but that in higher organisms both are contained in one nucleus. The trophochromatin may in the latter case be extruded in the form of chromidia, which are therefore analogous to the trophic meganucleus of the infusoria. This "binuclearity hypothesis" is not widely favored today.

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[1] See on this subject E. V. Cowdry (1924), Duesberg (1911), Dobell (1909, 1911*a*), Agar (1920).

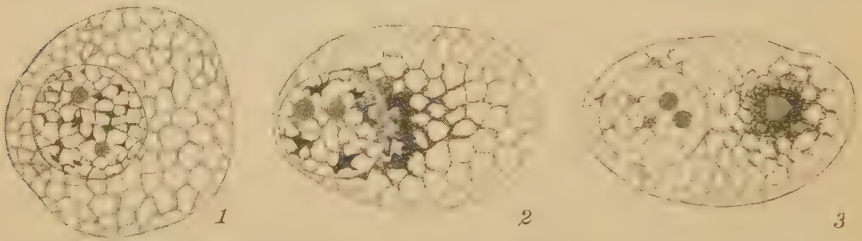

FIG. 102.—Chromidia in mesenchyme cell of sea-urchin. 1, preëmission stage. 2, emission of chromidia from nucleus. 3, postemission stage; skeletal element forming in midst of chromidial mass. (*After Schaxel*, 1910.)

Following Hertwig, chromidia were described in many types of animal cells by a number of other investigators,[1] by no means all of whom, however, subscribed to the views of Hertwig and Goldschmidt regarding their origin and significance. They were observed in various somatic tissues, and appeared to be particularly conspicuous in oöcytes and spermatocytes, where a considerable mass of them develops near the nucleus during the growth period in the prophase of the first meiotic division. Typical drawings from a paper of this period are shown in Fig. 102. It was rather generally thought that such accumulations were simply granules of chromatin derived from the nucleus, and some workers indicated the nucleolus as the site of their origin. When special methods for the study of chondriosomes developed, however, it became apparent that chondriosomes, chromidia, secretion droplets, and other cytoplasmic

[1] Marcus (1907), Wassilief (1907), Popoff (1907, 1910), Reichenow (1908), Nowikoff (1909), Buchner (1909), Moroff (1909, 1911), Schaxel (1910–1912), M. Jörgensen (1910, 1913), Nussbaum (1913), Hirschler (1913), van Herwerden (1913).

bodies had been hopelessly confused, and that many of the elements which had passed as chromidia were, in reality, other materials for which there was no evidence of nuclear origin (Jörgensen, 1913*c*; Nussbaum, 1913). Lundegårdh (1910) showed that even leucoplasts had been mistaken for extra-nuclear karyotin in *Vicia* root cells. The identity of chondriosomes and chromidia was frequently claimed, statements being made that chondriosomes were "merely chromidia" or that chromidia were "merely chondriosomes." It has now been shown, however, that the chromidia are composed of nucleoprotein and the chondriosomes of phospholipin, so that their fundamental distinctness is assured.[1]

Although much of the evidence for the nuclear derivation of chromatic bodies in the cytoplasm has been shown to be of doubtful value, the question of their origin still remains unanswered. The view of Buchner, Schaxel, and others that the granules are transferred bodily through the nuclear membrane has not been well substantiated, but that a nucleic acid compound passes the membrane in solution, takes the form of granular "chromidia" as it reaches the cytoplasm, and is transformed into strands and clumps on fixation, is highly probable (van Herwerden, 1913). In hybrid echinoderm eggs Tennent (1920) finds that a definite cycle is passed through after insemination: the nucleus is at first strongly basophile; as the nucleus becomes paler a cloud of fine basophilic granules appear in the cytoplasm near-by; these become rod-shaped and soon scatter throughout the cytoplasm. The process is then reversed, the rods moving toward the nucleus, resuming the form of fine granules, and finally disappearing as the nucleus again becomes basophile. These chromatic bodies Tennent does not regard as chromidia, but as the result of an action of nuclear enzymes on the cytoplasm; and he is uncertain as to the application of this hypothesis to the chromatic bodies in non-hybrid cells. Such an evident transfer of basophilic substance from the cytoplasm to the nucleus was seen also by Danchakoff (1916), who observed that chromatic accumulations on the inner surface of the nuclear membrane occurred just at the points where the basophilic substance was most conspicuous outside; and she concluded that the chromatin of the nucleus is differentiated at least in part at the expense of a basophilic substance in the cytoplasm.

These observations are of interest not only because of the light they throw upon the problem of chromidia, but also because they afford visible evidence of an interchange of materials between nucleus and cytoplasm, such interchanges obviously being of the highest importance in protoplasmic activity. Such basophilic substances appear to be in some way concerned with the Nissl bodies of nerve cells and the basal filaments of certain gland cells (see Cowdry, 1924), but their true relation to the chromatic nuclear substance and the bodies originally called chromidia in the Protozoa has yet to be elucidated. For the present it seems well to speak of such basophilic nucleo-proteins in the cytoplasm as chromidial substance, leaving it to the future to determine the significance of the forms in which it may appear.

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[1] Duesberg (1910–1912), Schaxel (1911*c*), Hirschler (1913), Jörgensen (1913*c*), E. V. Cowdry.

**Karyotin Extrusion in Plants.**—A number of botanists have observed remarkable extensions or extrusions of karyotin from the nucleus in fixed preparations of plant cells, particularly sporocytes.[1] Such extruded karyotin may form deeply staining globules or irregular masses in the cytoplasm, often with clear areas about them. Frequently it appears as a chromatic prolongation extending from the nucleus into the cytoplasm, or even through the wall into an adjacent cell, where it forms a terminal swelling. Schürhoff observed a case in which the prolongation passed completely through the adjacent cell into one beyond.

Agreement has not been reached on the question of the significance of such phenomena. It may be expected that materials passing from nucleus to cytoplasm will at times be visible as globules at the nuclear surface, and some observers (*e.g.*, West and Lechmere) have been inclined to view the more pronounced extrusions and extensions of karyotin also as indications of a normal process. The tendency at present, however, is to regard such extreme nuclear behavior as something very abnormal.[2] It has been variously attributed to rough handling, poor fixation, wound reactions, and degenerative or pathological conditions. There is much to support this interpretation in the earlier observations of Hottes (1901), Miehe (1901), Schrammen (1902), and Némec (1904, 1910) on the changes in position and shape undergone by nuclei in tissues which had been wounded or placed in abnormal environments. Although one may, therefore, question the occurrence of the exaggerated extrusions of karyotin in normally functioning tissue, it is possible that such nuclear reactions may throw some light on the causes of normal nuclear movements, as, for example, in syngamy.

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[1] Körnicke (1901) for *Crocus;* Schürhoff (1906) for *Iris;* Digby (1909, 1910, 1912, 1914) for *Galtonia, Primula,* and *Crepis;* Gates (1911) and Gates and Thomas (1914) for *Œnothera;* Gates (1920) and Gates and Rees (1921) for *Lactuca;* West and Lechmere (1915) for *Lilium;* Modlewski (1918) for *Neottia;* Sakamura (1916, 1920) for *Vicia;* Yasui (1921) for *Papaver;* Sinotô (1921, 1922*a*) for *Iris;* Tischler (1921) for *Phragmites;* de Litardière (1925*c*) for *Podophyllum.* For a more complete review, see Tischler (1921–1922).

[2] This is the opinion of the last six workers named in the preceding footnote.

# CHAPTER XIII

# MEIOSIS

The subject of meiosis is of the utmost importance in cytology. Many of the problems, both theoretical and practical, upon which biologists are expending their most intense efforts seem to be bound up directly or indirectly with this process. The essential feature of meiosis is relatively simple in nature, and must be thoroughly grasped in order that the discussions in the following chapters may be intelligible. The entire process by which the essential change is accomplished, on the contrary, is very complicated and extremely difficult to observe and interpret with any degree of confidence. In spite of the enormous amount of work already done, there still exists much difference of opinion regarding some of the most significant steps in the alteration undergone by the nuclear material. In the present chapter a number of these opinions will be reviewed, but our main purpose will be to make clear the fundamental feature of meiosis.

In an earlier chapter it was shown that each somatic nucleus contains a complement of chromosomes which are definite in number, and which often indicate functional differentiations in their characteristic differences in size and form. In the bodies of higher organisms, as well as at certain stages in the life cycles of most lower organisms, the chromosomes are present in the *diploid* number: the complement is composed of two intermingled *haploid* sets of chromosomes which were brought together in the previous union of gametes. In meiosis there is accomplished what has long been referred to as "the reduction of the chromosomes." This expression has had two meanings. In the first place, it has meant the change from the diploid to the haploid number which occurs at this time, a change which is frequently called "numerical reduction." In the second place, it has been applied more specifically to the disjunction of the two members of each pair of corresponding ("homologous") chromosomes present in the diploid complement, an event which constitutes the central feature of meiosis. It will be possible to avoid much ambiguity in the following discussions by using the terms *haplosis*[1] for

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[1] The terms *haplosis* and *diplosis* have been suggested by McClung for the halving of the chromosome number in meiosis and the doubling of the number in syngamy. In hybrids between forms with unequal chromosome numbers, and in certain other organisms with more or less than the diploid number, it is obvious that the numerical changes may not be exact halving and doubling, as will be shown in Chapter XVII; but it is not thought that this will seriously impair the usefulness of the terms.

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numerical reduction and *disjunction* for the segregation of homologous elements. The divergence of the halves of an equationally split chromosome will be referred to as *separation.*

It should already be apparent that, because of the profound alterations in the chromosomal mechanism effected by meiosis and syngamy, these processes represent the two most important crises in the life cycle, so far as nuclear constitution is concerned. This will be even more evident after the significant changes have been examined in detail. Before turning to this task, however, it should be noted at what point in the life cycles of various organisms the meiotic alteration in the chromosome complement is accomplished.

**The Stage in the Life Cycle at Which Meiosis Occurs.**—Haplosis and chromosome disjunction are accomplished during the course of two nuclear divisions known as the *meiotic divisions.* Because of its peculiar appearance the first of these divisions was termed the "heterotypic" by Flemming (1887), while the second, which was seen to resemble a somatic division in many features, was called the "homœotypic." Although these terms are still widely used, certain advances in our knowledge of meiosis since the days of Flemming have led a number of cytologists to discontinue their use, and to refer simply to the *first* and *second* meiotic mitoses or divisions. They are also called "maturation divisions," especially in the case of maturing animal eggs. Since meiosis involves two mitoses, the resulting nuclei or cells are formed in groups of four (*quartets,* or *tetrads*)[1] although not all of the members of a quartet may function. For convenience the two meiotic mitoses will frequently be referred to in subsequent pages as *I* and *II.*

**In animals,** almost without exception, meiosis occurs in connection with gametogenesis (Fig. 103). In the male animal those cells (*spermatogonia*) in the testis whose ultimate descendants are to become spermatozoa multiply by divisions of the ordinary equational type until a certain number are produced. These cells, now called *primary spermatocytes,* enlarge and undergo two successive divisions: the first division results in two cells called *secondary spermatocytes;* the second divides the two secondary spermatocytes into four *spermatids,* each of which then becomes transformed into a *spermatozoön.* The four male gametes are therefore the direct result of the two meiotic divisions. Besides the spermatogenous cells, the testis also contains certain accessory cells, such as the Sertoli cells of mammals and the Verson's cells of certain insects.

In the female the situation is somewhat different: here nearly all of the differentiation of the gamete is accomplished before the meiotic nuclear divisions actually occur. The *primary oöcytes* (*ovocytes*) are the descendants of a number of generations of *oögonia* (*ovogonia*). The oöcyte, usually while its nucleus is in the prophase of the first meiotic division, enlarges greatly ("growth period"), becomes filled with stored food, and develops the general features characterizing the egg. The oöcyte is now called the "ovarian egg." Meanwhile some of the oögonia have developed various accessory cells. At a comparatively late stage, in many cases even after the spermatozoön has entered the egg at fertilization, the nucleus (*germinal vesicle*), having passed through some of the prophasic changes characteristic of the first meiotic mitosis before and during the growth period, gives rise to a mitotic figure which is often surprisingly small for the volume of the nucleus. The spindle takes up a position perpendicular to the surface of the cell, and in the telophase the chromosomes passing to the outer pole are included in the *first polocyte*, or *polar body*, a small cell cut off at this point (Fig. 165). A second spindle is rapidly formed about the chromosomes remaining in the egg (called at this stage the *secondary oöcyte*) and the second meiotic mitosis occurs, one daughter nucleus being included in the *second polocyte*, or *polar body*. In the course of these two divisions haplosis is accomplished. The first polocyte may divide to form two, thus completing the quartet of cells corresponding to the quartet of spermatozoa in the male. Although the polocytes are normally functionless, they are generally

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[1] "Quartet" is the preferable term. Although "tetrad" has been much more commonly used, it will conduce to clearness if we restrict its application to chromosomal tetrads, which we shall soon discuss.

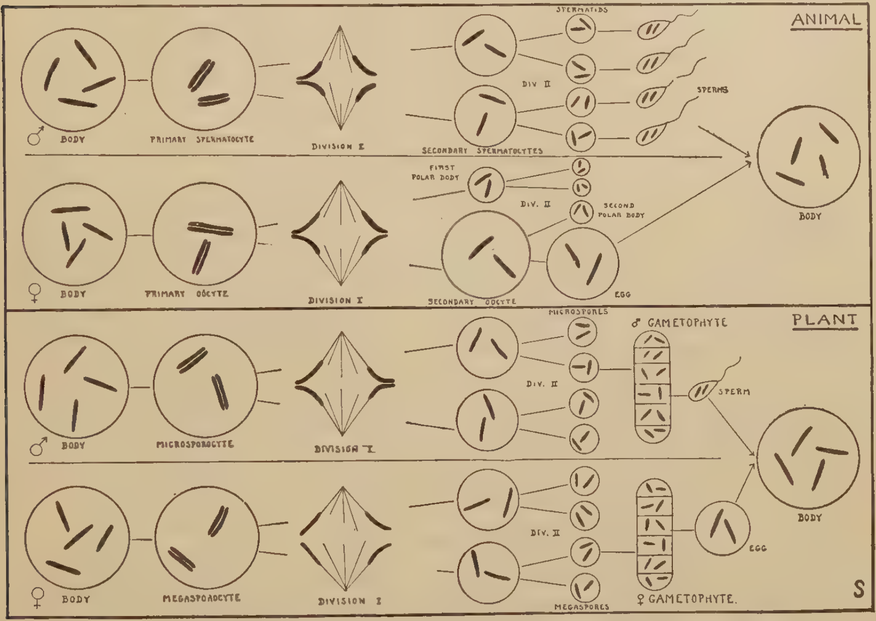

FIG. 103.—Diagram showing the history of the chromosomes in the ordinary life cycles of animals and plants.

looked upon as eggs historically: the meiotic divisions probably resulted formerly in a quartet of eggs, whereas only one relatively large and highly differentiated egg is now produced at the expense of the other three cells, which remain small and functionless.

In the Protozoa meiosis essentially like that in the Metazoa has been described in a number of instances, although the morphology of the structures involved differs greatly. In some of these cases meiosis occurs immediately before sexual fusion, as in Metazoa, whereas in others it takes place afterward (Dobell, 1925, on Sporozoa). Other forms show peculiar modes of nuclear behavior whose relation to meiosis is uncertain.[1]

**In plants** it has been found that meiosis occurs regularly at sporogenesis in bryophytes and vascular plants, but at several other stages of the life cycle in different members of the lower groups. Considering first the myxomycetes, it has been claimed by Olive (1907) and Jahn (1908) that in *Ceratiomyxa* spore formation is accompanied by haplosis. Nuclear fusions are seen in the plasmodium, after which there are two mitoses that appear to reduce the chromosome number from 16 to 8; a spore is then formed about each haploid nucleus. In *Trichia* and *Arcyria* meiosis is also said to follow nuclear fusions in the plasmodium (Kränzlin, 1907.) In *Plasmodiophora brassicæ,* according to Prowazek (1905), the plasmodium breaks up into uninucleate masses which fuse in pairs and become spores with two nuclei each. These nuclei in two mitoses give off "reduction nuclei," leaving two haploid sexual nuclei which then fuse. In this species, therefore, the sexual nuclei are the only haploid ones in the cycle, whereas in the preceding cases the zygote nucleus is the only diploid one.

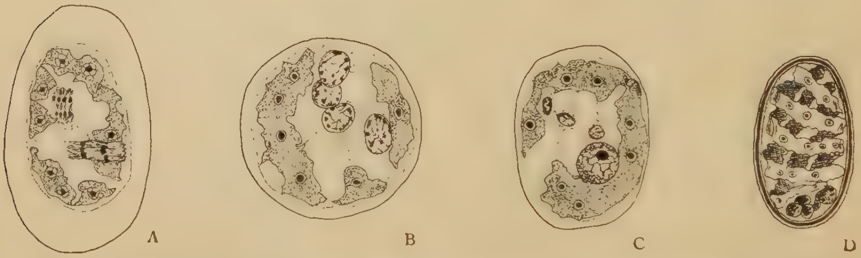

FIG. 104.—The behavior of the nuclei and plastids in the zygospore of *Spirogyra. A, S. calospora;* second meiotic mitosis. *B,* four nuclei resulting from meiosis in *S. longata. C,* degeneration of 3 of the 4 meiotic nuclei in *S. longata. D,* degeneration of plastids contributed by ♂ gamete in *S. neglecta.* (*After Tröndle,* 1911.)

In the green algæ it is in the first two divisions of the zygote (either a zygospore or an oöspore) that haplosis is accomplished. This has been definitely established in *Spirogyra* (Karsten, 1908; Tröndle, 1911) (Fig. 104), *Zygnema* (Kurssanow, 1911), *Coleochæte* (C. E. Allen, 1905*c*)

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[1] See Minchin (1912), Jennings (1920), Kofoid (1923), Morgan *et al.* (1922).

*Cylindrocystis* (H. Kauffmann, 1914), and *Volvox* (W. Zimmermann, 1921). In a number of other genera, such as *Ulothrix, Œdogonium, Sphæroplea,* and *Closterium,* in which the chromosomes are not so well known, it is probable that the same condition exists, since the zygote upon germination gives rise with considerable regularity to four cells or nuclei; in some cases (*Œdogonium*) the four cells are zoöspores. Since meiosis follows immediately upon syngamy, the vegetative bodies of these organisms contain the haploid number of chromosomes in their nuclei.[1] *Chara,* according to Oehlkers (1916), conforms to this scheme, the zygote giving rise upon germination to four haploid nuclei, of which three degenerate, as is also the case in *Spirogyra.* Tuttle (1924), however, has recently reported briefly that in *Nitella* meiosis takes place in the apical cells of the oögonia and antheridia, the vegetative body being a diplont rather than a haplont. Confirmation of this reported difference between two closely related genera is naturally awaited with interest. The diatom, *Surirella saxonica,* is also a diplont, meiosis occurring in the formation of the gamete nuclei (Karsten, 1912). There is evidence that the same is true of other diatoms.

Among the brown algæ meiosis occurs in connection with zoöspore formation in *Cutleria-Aglaozonia* (Yamanouchi, 1912), *Zanardinia* (Yamanouchi, 1913*b*), *Ectocarpus* (Kylin, 1918), and *Pylaiella* (Knight, 1923). In *Dictyota* (J. Williams, 1904) and *Padina* (Wolfe, 1918) it takes place in the divisions giving rise to the tetraspores, as in the red algæ, among which these genera are sometimes classified. An exceptional situation is found in *Fucus:* here haplosis occurs in the divisions immediately following the delimitation of the stalk cells of the antheridium and the oögonium. Since there are only three divisions and therefore eight eggs in the oögonium, these eggs are but one division removed from the four products of the meiotic mitoses, a condition closely approaching that in animals. That *Fucus* is thus a diplont producing haploid gametes was inferred by Strasburger and Farmer and Williams, and demonstrated by Yamanouchi (1909).

In red algæ with tetraspores in the life cycle meiosis occurs in the two mitoses which differentiate the nuclei of these spores. This has been shown for *Polysiphonia* (Yamanouchi, 1906), *Griffithsia* (I. F. Lewis, 1909), *Nitophyllum* (Svedelius, 1914*ab*), *Delesseria* (Svedelius, 1914*c*), and *Corallina* (Yamanouchi, 1913*c*, 1921). In *Scinaia* (Svedelius, 1915) and

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[1] Organisms with the haploid number of chromosomes in each somatic nucleus are known as *haplonts,* and those with the diploid number as *diplonts.* The haploid and diploid phases of any life cycle are called, respectively, the *haplophase* and *diplophase* (Goebel), or *gamophase* and *zygophase* (Winkler). In plants with two well-marked "generations" (*gametophyte* and *sporophyte*) in the life cycle the *alternation of generations* usually, but not always, coincides with the *alternation of nuclear phases.* Exceptions to the general rule will be dealt with in Chapter XVI.

*Nemalion* (Cleland, 1919), which have no tetraspores, it occurs as the zygote germinates, as in so many green algæ.[1]

In the ascomycetes a binucleate condition of the cells arises in the archicarp (see p. 324), from which ascogenous hyphæ grow out. As these hyphæ grow the binucleate condition is maintained by the simultaneous ("conjugate") division of the nuclei before every cell-division. When the ascus is finally developed (Fig. 155, *A*) its two nuclei fuse, forming the diploid "primary ascus nucleus." This nucleus then undergoes three successive divisions, giving rise to eight nuclei about which the ascospores are organized. Haplosis takes place in the course of the first two of these mitoses. It was for a long time generally thought that there were two nuclear fusions in the life cycle: one in the archicarp and another in the ascus, and the three mitoses in the ascus were regarded as a means of reducing the quadrivalent chromosomes to a univalent condition (Harper, 1905; J. B. Overton, 1906). Such a "double reduction" was described (Fraser, 1907, 1908) for *Humaria rutilans;* the third mitosis was said to be "brachymeiotic," bringing about a second reduction in addition to that accomplished by the first two mitoses.[2] Harper (1900, 1905), although he thought two fusions occurred, found no double reduction, holding rather that the fusion of the two ascus nuclei and their chromosomes was so complete that their quadrivalent nature was wholly invisible. Faull (1905, 1912), Claussen (1912), W. H. Brown (1909, 1910), Bagchee (1925), and others also found only a single reduction in a number of species, the third mitosis being purely equational. Furthermore, the researches of these and other investigators (see p. 325) have made it highly probable that there is but one nuclear fusion in the life cycle—that in the ascus—thus removing the apparent necessity for a second reduction.

In the basidiomycetes there is commonly a nuclear fusion in the basidium, though the origin of the binucleate condition in the hyphæ has until recently been somewhat obscure (see p. 326). Haplosis occurs as the diploid fusion nucleus divides to form the four basidiospore nuclei (Fig. 105). As in the ascomycetes, therefore, it follows immediately upon nuclear fusion—in the basidium in hymenomycetes and in the teliospore in rusts.[1] An exception to this rule is known in the case of carpophores occasionally produced by unisexual mycelia without hyphal conjugation (p. 326).

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[1] For general reviews of reproduction and alternation of generations in the algæ, see Bonnet (1914), Janet (1914), and Oltmanns (1922–1923). Davis (1916) gives a convenient summary of the life histories of the red algæ. Dodge (1914) summarizes and compares the life cycles of red algæ and ascomycetes. Researches on ascomycetes are reviewed by Atkinson (1915). Guilliermond (1913*e*) reviews the subject of fungus cytology; see also his book on the yeasts (1920*n*). For further discussions of alternation of generations and nuclear phases, see the works cited in the footnote at the beginning of Chapter XVI. A general account of meiosis in all plant groups is given by Tischler (1921–1922, Chapter 6).

[2] Also in *Otidea aurantia* and *Peziza vesiculosa* (Fraser and Welsford, 1908); *Lachnea stercorea, Ascobolus furfuraceus,* and *Humaria granulata* (Fraser and Brooks, 1909); and *Helvella crispa* (Carruthers, 1911).

In the normal life cycles of all bryophytes, so far as known, meiosis normally occurs in the two mitoses which differentiate the nuclei of each quartet of spores.[2]

In vascular plants, as in bryophytes, meiosis in all normal life cycles occurs in the divisions which give rise to the nuclei of the spore quartets (Fig. 103). The spore on germination produces the gametophyte generation. In the case of forms with microspores and megaspores (some pteridophytes and all seed plants) this is a much abbreviated phase in the life cycle, so that meiosis closely precedes the differentiation of the gametes in such cases. There is considerable diversity in the mode of development in the seed plants, but the prevailing situation in the angiosperms is as follows:

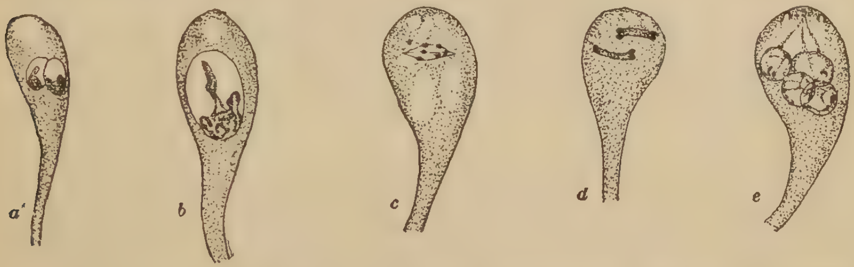

FIG. 105.—Sexual nuclear fusion and the meiotic mitoses in the basidium of *Nidularia pisiformis*. (*After Fries*, 1911.)

In the anther the sporogenous cells multiply for a time and eventually enter the prophase of the first meiotic division. These cells in which meiosis is initiated are known as *microsporocytes;* they usually round up more or less from one another at this stage and float freely in a liquid. The two meiotic mitoses now occur in rather rapid succession (Fig. 106). In some cases a wall is formed after the first mitosis, giving secondary microsporocytes, but more commonly cytokinesis does not occur until after the second mitosis, when the cell is divided simultaneously by furrows or otherwise into four *microspores*. Each microspore, which has the reduced number of chromosomes, develops a thick wall, and soon forms a very simple male gametophyte. It first divides into a tube cell and generative cell, the latter dividing again to form the two male gametes. It is of interest to add that in sections of certain elongated anthers, such as those of *Lilium*, the various stages in the meiotic divisions may sometimes be observed in their natural sequence by passing from the end of the anther toward the middle, or from one end to the other. In *Zea* the successive stages are seen simultaneously not within a single anther, but in successive flowers beginning at the base or apex of a branch of the inflorescence and passing toward a point near the middle. Such facts are frequently of service in determining the proper seriation of problematic phases.

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[1] Shown by Juel (1898*a*), Maire (1905*b*), Guilliermond (1910), Kniep (1911, 1913), Levine (1913), and others for hymenomycetes; by V. H. Blackman (1904), Dietel (1911), Fitzpatrick (1918), and others for rusts; and by Gilbert (1922) for *Dacromyces.* A summary of researches on rusts up to 1911 is given by Maire (1911). See also Tischler (1921–1922).

[2] Farmer (1894, 1895) and A. C. Moore (1903, 1905) on *Pallavicinia;* B. M. Davis (1899, 1901) on *Anthoceros* and *Pellia;* Walker (1913) and Vandendries (1913) on *Polytrichum;* Melin (1915) on *Sphagnum;* C. E. Allen (1917*b*, 1919) and Schacke (1919) on *Sphærocarpos;* Florin (1918*a*) on *Chiloscyphus.*

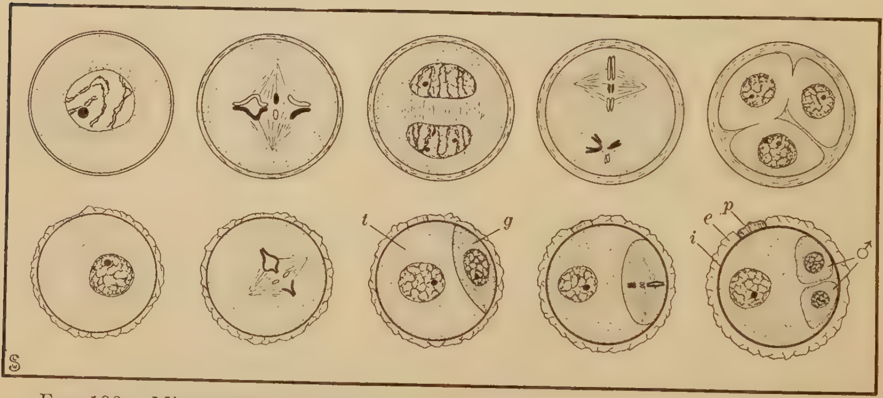

FIG. 106.—Microsporogenesis and the development of the male gametophyte in an angiosperm. First row: the two meiotic mitoses in the microsporocyte, followed by a cleavage of the protoplast into 4 spores, 3 of which are shown. Second row: formation of male gametophyte by one microspore. *t*, tube cell; *g*, generative cell; ♂, male gametes; *i*, intine; *e*, exine; *p*, germ pore with plug. Semi-diagrammatic.

In the ovule a single *megasporocyte* is developed by the enlargement of a subepidermal cell of the nucellus (Fig. 107). At the close of the first meiotic mitosis a wall is formed between the nuclei, and the two resulting cells (secondary megasporocytes) divide again, giving thus four *megaspores*. (In some cases the outer secondary megasporocyte does not divide.) The outer three megaspores disintegrate, while the innermost enlarges to form the "embryo sac," its nucleus by a series of three free

FIG. 107.—Megasporogenesis, development of female gametophyte, syngamy, and early embryogeny in an angiosperm. 1–5, division of megasporocyte into linear quartet of megaspores; meiosis occurs in the two mitoses. 6–12, development of female gametophyte by innermost megaspore, this involving 3 mitoses. In the upper end of the embryo sac in 12 the largest cell is the egg; the two polar nuclei are in the center. 13, discharge of 2 ♂ nuclei into embryo sac by pollen tube. 14, double fertilization, one ♂ nucleus fusing with egg nucleus, the other with polar nuclei. 15, embryo in 2-cell stage; endosperm in cœnocytic stage. 16, embryo has developed cotyledons, and endosperm has become cellular. Semi-diagrammatic.

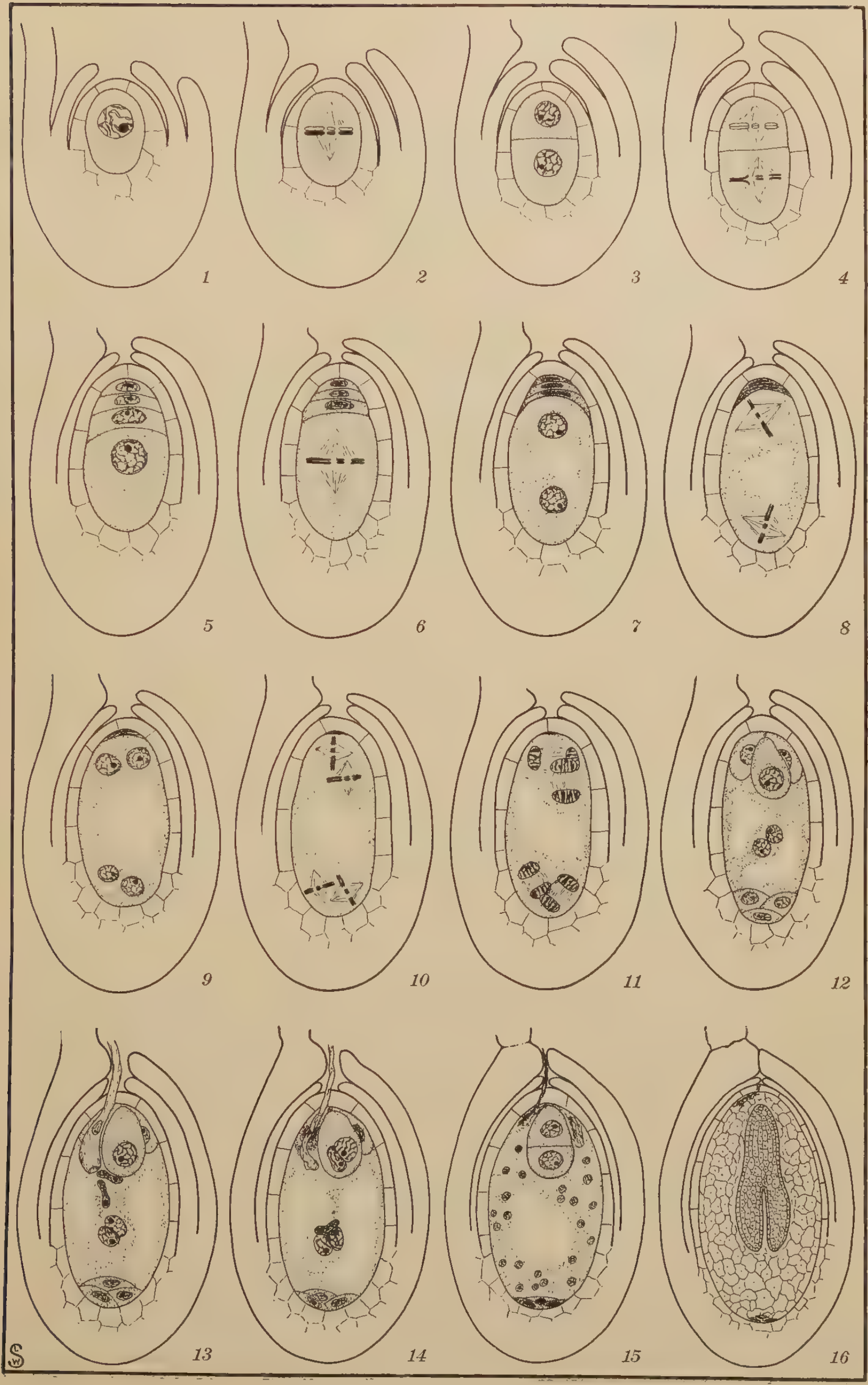

FIG. 107.

divisions giving rise to eight. The female gametophyte consists of the sac cytoplasm with the eight nuclei, about some of which cell membranes develop. Commonly one *egg* and two *synergids* are formed in the micropylar end of the sac, while a group of three *antipodal cells* occurs in the chalazal end. The remaining two *polar nuclei* unite to form a polar fusion nucleus, a male nucleus usually being added also (p. 331). In such a typical embryo sac, therefore, the gamete nucleus is removed from the immediate product of meiosis (megaspore nucleus) by three mitoses (see also Fig. 108).

Many variants of the process just described have been found in angiosperms.[1] Several of these are diagrammed in Fig. 108. Probably the commonest of such unusual modes of development is that exemplified by *Lilium:* here no walls are formed after either meiotic mitosis, the four nuclei lying free in the cytoplasm of the embryo sac, where they undergo one further mitosis to form a typical eight-nucleate gametophyte (Sargant, 1896). The egg, therefore, is here removed from the product of meiosis by a single mitosis. A condition intermediate between this and the usual one is seen in *Smilacina*, where the walls form and then disappear, leaving the four nuclei to divide to eight (McAllister, 1909). Of exceptional interest is the situation in *Plumbagella micrantha*, described by Dahlgren (1915). Here the four nuclei, formed freely as in *Lilium*, divide no further; one of them becomes directly the nucleus of the egg, two of them fuse like polar nuclei, and the fourth disintegrates in the base of the sac. This is the only known case among higher plants in which the gamete is the immediate product of meiosis, as in animals. No case of a similar derivation of the male gamete is yet known.

In several known instances the embryo sac is developed neither from a single megaspore as in the usual type, nor directly from the primary megasporocyte as in *Lilium* and *Plumbagella*, but from one of the secondary megasporocytes. In *Cypripedium*, for example, the nucleus of this cell undergoes the second meiotic mitosis, after which another mitosis occurs, giving four nuclei, one of which becomes the nucleus of the egg (Pace, 1907). Embryo sacs with more than eight nuclei have also been found. In *Peperomia hispidula* no walls are formed after the meiotic mitoses, the four nuclei dividing twice in succession to give 16. An egg and one synergid are organized, and the remaining 14 nuclei fuse (D. S. Johnson, 1907). In *Euphorbia virgata* the 16 nuclei arise from a single megaspore nucleus, which therefore initiates a series of four mitoses

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[1] See the summary by Rutgers (1923); also Stenar (1925).

FIG. 108.—Diagram showing how the nuclei resulting from meiosis are involved in the development of the female gametophyte in various angiosperms. The 4 meiotic nuclei are shown in black (third column), and the nucleus of the ♀ gamete is marked with cross lines. Each series begins with the megasporocyte and ends with the mature female gametophyte.

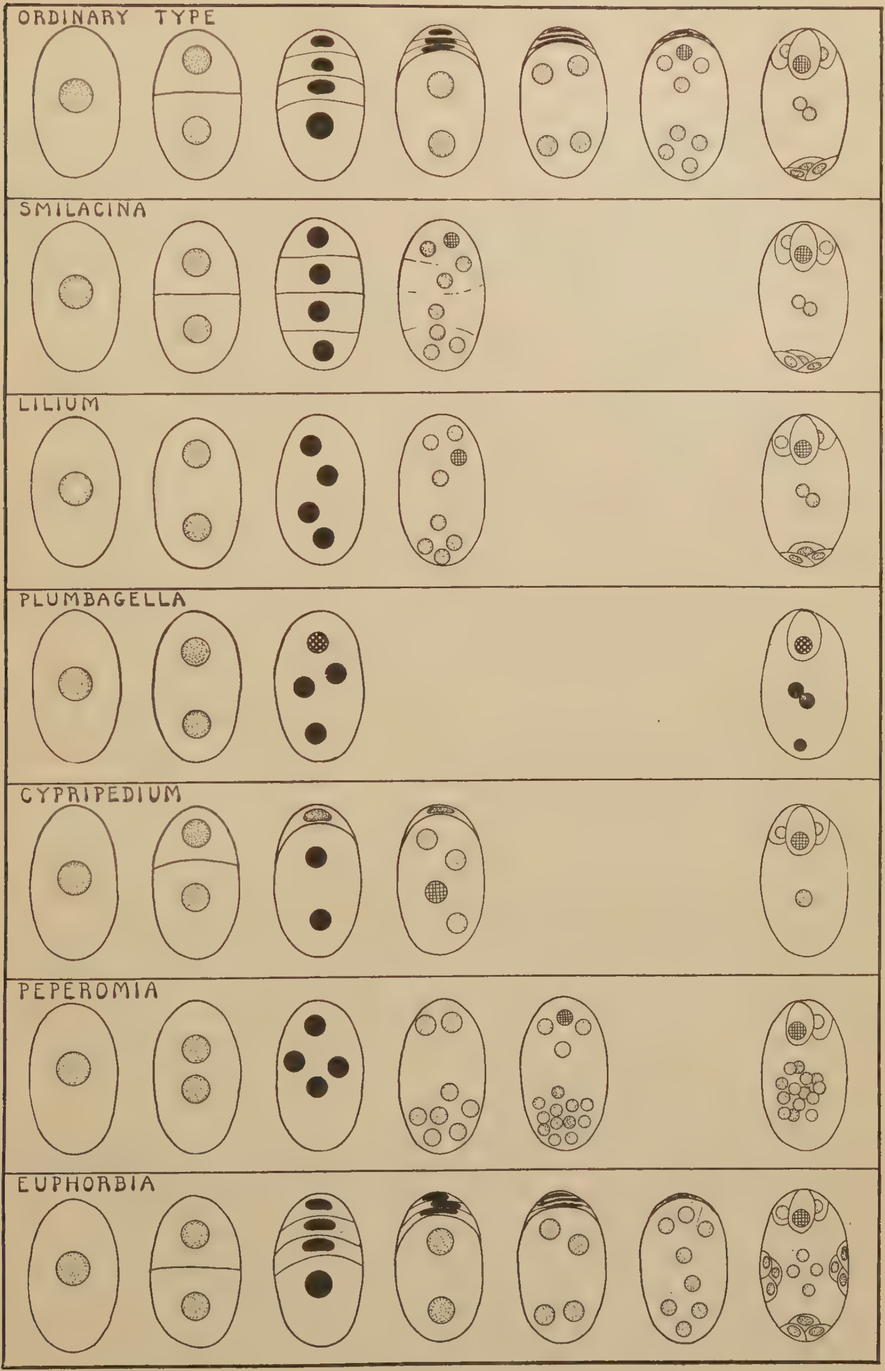
ORDINARY TYPE
SMILACINA
LILIUM
PLUMBAGELLA
CYPRIPEDIUM
PEPEROMIA
EUPHORBIA

FIG. 108.

rather than three as in the ordinary type of development. Three groups of three cells each are formed, and the remaining four nuclei fuse (Dessiatoff, 1911).

The importance of these facts for the geneticist will be more apparent after the relation of meiosis to the segregation of the factors of inheritance has been discussed. It will be sufficient here to call attention to the fact that when all of the embryo sac nuclei arise from one of the four products of meiosis, they may be assumed to be of the same genetic constitution; but when they are derived from more than one, as in several of the examples cited above, they may differ greatly, so that very unusual correlations between the characters of the sporophyte and those of the endosperm may be expected. In several instances two or more of the described modes of development are known to occur in the same family, and even in the same individual.

The term *gonotokont* was introduced by Lotsy (1904) to designate any cell, whatever its origin or position in the life cycle, in which the meiotic process is initiated. The gonotokonts are therefore the spermatocyte and oöcyte in animals, the zygote in most green algæ, the tetrasporocyte in some red algæ and the zygote in others, the young oögonial and antheridial cells in *Fucus*, the ascus in ascomycetes, the basidium in basidiomycetes, and the sporocytes in bryophytes and vascular plants. Similarly, the immediate products of meiosis are known as *gones;* these are consequently the gametes in animals and the spores in most plants.

**The Meaning of Meiosis.**—In order that the true meaning of meiosis may be made clear it will be well to indicate the main points of an influential theory first suggested by Roux (1883) and later developed particularly by Weismann (1887, 1891, 1892). It had been thought by those who first saw the reduction in chromosome number (see Chapter I) that the function of the process was simply "to prevent a summation through fertilization of the nuclear mass and of the chromatic elements" (Hertwig, 1890). But the chromatic mass is actually quartered in meiosis, whereas the number of chromosomes is halved. Moreover, great changes in nuclear volume occur with no change in the number of chromosomes. This careful guarding, so to speak, of the chromosome number was seized upon as a most significant fact by Roux, who "argued that the facts of mitosis are only explicable under the assumption that the chromatin is not a homogeneous substance, but differs qualitatively in different regions of the nucleus; that the collection of the chromatin into a thread and its accurate division into two halves is meaningless unless the chromatin in different regions of the thread represents different *qualities* which are to be divided and distributed to the daughter cells according to some definite law. He urged that if the chromatin were qualitatively the same throughout the nucleus, direct division would be as efficacious as indirect, and the complicated apparatus of mitosis would be superfluous."[1] Upon this conception Weismann based his remarkable theory, the starting point of which was

> . . . the hypothesis of de Vries that the chromatin is a congeries or colony of invisible self-propagating vital units or *biophores*, somewhat like Darwin's "gemmules," each of which has the power of determining the development of a particular quality. Weismann conceives these units as aggregated to form units of a higher order known as "determinants," which in turn are grouped to form "ids," each of which . . . is assumed to possess the complete architecture of the germ-plasm characteristic of the species. The "ids" finally, which are identified with the visible chromatin-granules, are arranged in linear series to form "idants" or chromosomes. It is assumed further that the "ids" differ slightly in a manner corresponding with the individual variations of the species, each chromosome therefore being a particular group of slightly different germ-plasms and differing qualitatively from all the others.

We come now to the essence of Weismann's interpretation. The end of fertilization is to produce new combinations of variations by the mixture of different ids. Since, however, their number, like that of the chromosomes which they form, is doubled by the union of two germ-nuclei, an infinite complexity of the chromatin would soon arise did not a periodic reduction occur. Assuming, then, that the "ancestral germ-plasms" (ids) are arranged in a linear series in the spireme thread or the chromosomes derived from it, Weismann ventured the prediction (1887) that two kinds of mitosis would be found to occur. The first of these is characterized by a longitudinal splitting of the thread, as in ordinary cell-division, "by means of which all the ancestral germ-plasms are equally distributed in each of the daughter-nuclei after having been divided into halves." This form of division, which he called *equal division* (Aequationstheilung), was then a known fact. The second form, at that time a purely theoretical postulate, he assumed to be of such a character that each daughter-nucleus should receive only half the number of ancestral germ-plasms possessed by the mother-nucleus. This he termed a *reduction division* (Reduktionstheilung), and suggested that this might be effected either by a *transverse* division of the chromosomes, or by the elimination of entire chromosomes without division. By either method the number of "ids" would be reduced; and Weismann argued that such reducing divisions must be involved in the formation of the polar bodies, and in the parallel phenomena of spermatogenesis.

*Synapsis and Disjunction.*—As would be expected, there were soon announced certain interpretations of chromosome behavior based on Weismann's idea. Several cytologists thought that they found the chromosomes actually dividing transversely at one or the other of the meiotic mitoses. This interpretation, however, proved to be incorrect. Much light was thrown on the problem when Henking (1890–1892), Rückert (1891, etc.), Haecker (1890–1899), vom Rath (1892–1893), and others showed that the double chromosomes appearing in the reduced number at the first mitosis are not split chromosomes like those seen in somatic divisions, but are pairs of chromosomes, or *bivalent chromosomes*, each arising by an end-to-end conjugation of two somatic chromosomes. This conjugation is known as *synapsis*, or sometimes as *syndesis*. The two "synaptic mates" then *disjoin* at one of the meiotic mitoses. In this way the whole complement of chromosomes is assorted into two groups, each with the reduced number. It is in the light of this bivalent chromosome conception that one should interpret the many early reports of a transverse division of the chromosome during meiosis. What was called a transverse division was merely the disjunction of two entire chromosomes placed end-to-end.

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[1] This and the following quotations are from Wilson (1900, pp. 245–246).

A number of workers soon found that in many cases there is nothing even simulating a transverse division, either of single chromosomes or of bivalent pairs, but that both meiotic divisions are apparently longitudinal.[1] How, then, is there any "reduction in qualities?" This question was answered by a number of cytologists[2] who showed that in such cases the chromosomes conjugate side-by-side rather than end-to-end. Thus when they move apart there is the appearance of a longitudinal division, but "reduction" is nevertheless accomplished, since entire chromosomes, and not the longitudinal halves of split chromosomes, are disjoining. The appearance of a longitudinal division may also be present after an end-to-end conjugation, for the two members may bend around to a side-by-side position before finally disjoining. As a matter of fact, the meiotic divisions in nearly all cases, especially those studied by botanists, are both longitudinal in appearance. It is now customary to refer to side-by-side conjugation as *parasynapsis*, and end-to-end conjugation as *telosynapsis*. The terms *parasyndesis* and *telosyndesis* are also used.

From the standpoint of the chromosomes as bodies composed of or carrying units with a special function in heredity, one may make the general statement that "reduction" in the sense of Weismann is primarily a reduction in the number of inheritance units present in any single nucleus, the meiotic divisions bringing about a distribution of the units to different nuclei. Since this is accomplished by the disjunction of entire chromosomes rather than by a transverse division of every chromosome as Weismann suggested, the number of chromosomes is reduced along with the number of units.

**Outline of the Meiotic Process.**—Before proceeding with a detailed description of meiosis it is necessary to have clearly in mind the essential features of the process, and the points in which the mitoses involved differ from mitosis in somatic tissues.

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[1] Flemming, Brauer (1893), J. E. S. Moore (1896), Meves (1896), Grégoire (1899, etc.), and others.

[2] Montgomery (1901), von Winiwarter (1900), Sutton (1902), Grégoire (1904, etc.), Boveri (1904), and others.

The diploid chromosome complement of a somatic nucleus in the case of higher plants and animals is composed of two haploid sets which were brought together in the previous fusion of gametes. The chromosomes composing each haploid set differ from one another, often visibly. Since there are thus two chromosomes of each kind in the diploid complement, this complement is said to be made up of a certain number of pairs of chromosomes. There is an abundance of evidence which indicates that the two members of any given pair have, in general, the same rôle in the life of the organism: they are *homologous.*

In the division of a somatic nucleus, as has been shown in a previous chapter, each and every chromosome of the complement splits longitudinally into two halves which pass to the two daughter nuclei. Both of these nuclei are therefore like the original nucleus in containing derivatives of all the chromosomes; hence somatic mitosis is said to be *equational.* This is illustrated in Fig. 109, first column.[1]

In the prophase of the first meiotic mitosis (as a rule) a synapsis of homologous chromosomes takes place, giving the haploid number of bivalent chromosomes. These vary in their subsequent behavior in different organisms. In many cases (Fig. 109, second column) the homologues disjoin in the first mitosis, one member of each synaptic pair passing to each pole. During the anaphase a longitudinal split becomes visible in the chromosomes, and it is along this line that separation occurs in the second mitosis. Each of the four resulting nuclei thus contains a haploid set made up of one chromosome of each kind. In such a case, therefore, the first mitosis is disjunctional, since it segregates the homologues, and the second is equational, since it involves simple longitudinal splitting.

In many cases, particularly in animals, both the plane of synapsis and that of the splitting may be visible in the prophase of the first mitosis, giving *tetrad chromosomes* (Fig. 109, third column). The four members of each tetrad (the *chromatids*) are distributed by the two meiotic mitoses to the four resulting nuclei. They may be so arranged in the achromatic figure that the division in the first mitosis is along the line of synapsis, as shown in the diagram; here the first mitosis is disjunctional and the second equational ("prereduction"). In some cases, however, the tetrads are so arranged that they divide along the plane of splitting in the first mitosis, which is therefore equational, and along the synaptic plane in the second, which is therefore disjunctional ("postreduction"). In still other cases it has been shown that some of the tetrads divide disjunctionally in the first mitosis while other tetrads in the same cell do so in the second (Fig. 110, *C*). Here each mitosis is both disjunctional

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[1] For the sake of uniformity and clearness we have arbitrarily chosen 3 and 6 as the haploid and diploid numbers in making this and most of the subsequent diagrams. *Crepis virens* has just such a chromosome complement.

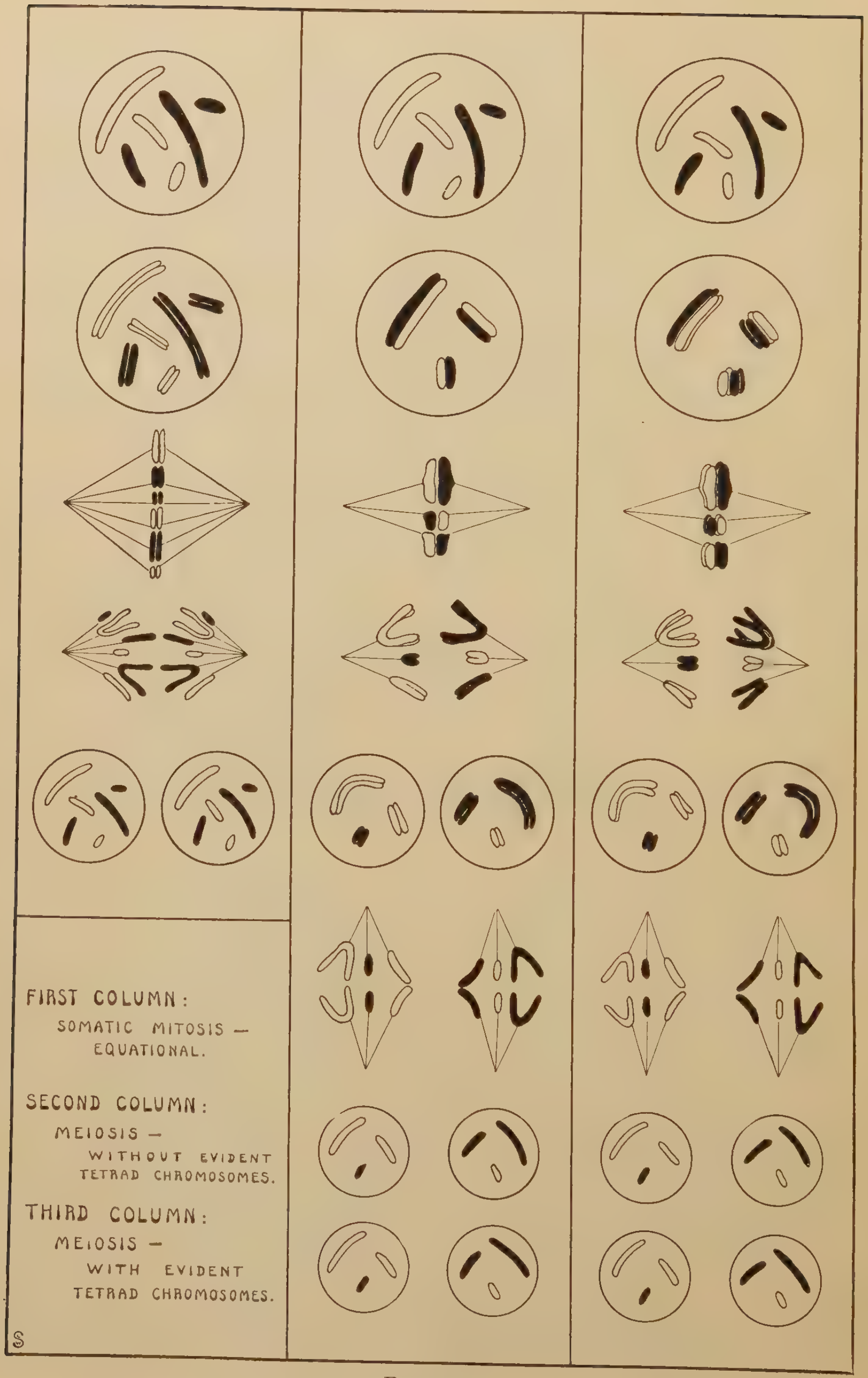
FIRST COLUMN:
SOMATIC MITOSIS —
EQUATIONAL.
SECOND COLUMN:
MEIOSIS —
WITHOUT EVIDENT
TETRAD CHROMOSOMES.
THIRD COLUMN:
MEIOSIS —
WITH EVIDENT
TETRAD CHROMOSOMES.

Fig. 109.

and equational—for different pairs of chromosomes. Reference will later be made to an additional complication, whereby it is thought that a single tetrad, as a result of "chiasmatypy," may in the same mitosis divide disjunctionally through one portion of its length and equationally through another portion.

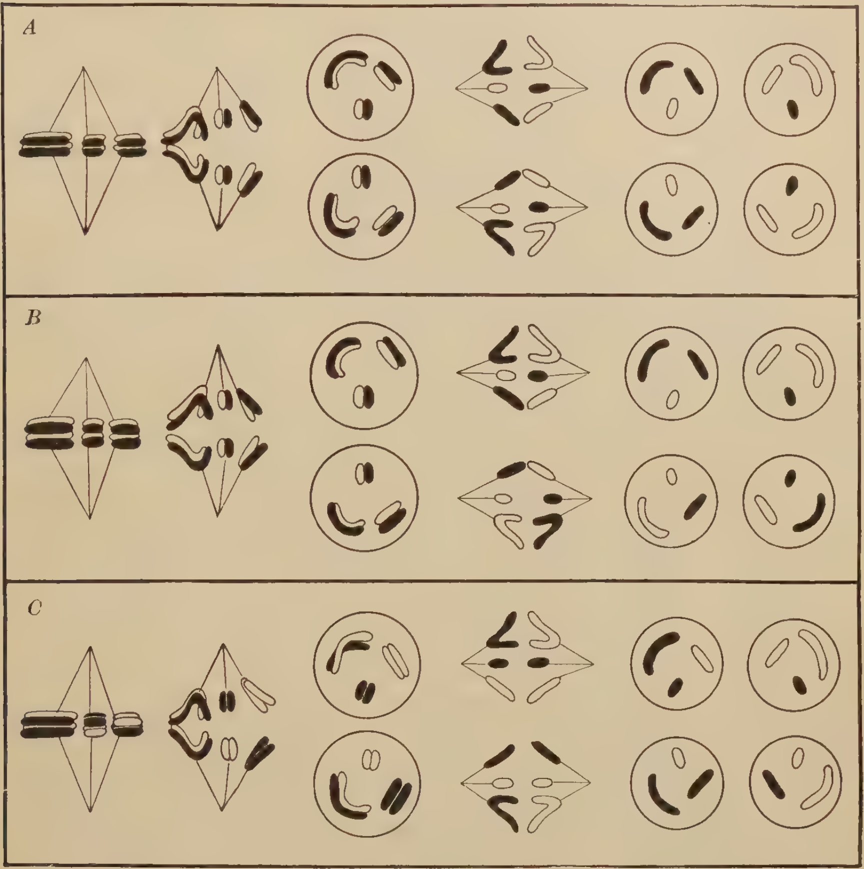

FIG. 110.—Diagram showing 3 ways in which the elements making up the tetrad chromosomes in a nucleus may be distributed to the 4 nuclei in meiosis. *A*, division *I* equational for all tetrads; chromosomes oriented alike in the two figures of division *II*; two kinds of nuclei in the resulting quartet. *B*, division *I* equational for all tetrads; chromosomes not oriented alike in the two figures of *II*; four kinds of nuclei in the quartet. *C*, division *I* equational for the large tetrad and disjunctional for the others; four kinds of nuclei in quartet. In Fig. 109 another mode of distribution is shown, all tetrads disjoining in *I*.

At the close of the two meiotic mitoses each of the four resulting nuclei has a haploid set made up of a longitudinal half of one member of each of the original chromosome pairs. If the three pairs be represented by the letters *Aa Bb Cc*, it is found that two of the four nuclei have *A* and the other two *a*; two have *B* and two *b*; two have *C* and two *c*. It is known that the various chromosome pairs are independently oriented and disjoined in meiosis,[1] so that, although a given nucleus of the quartet contains but one member of each pair, it may have any one of eight possible combinations: *ABC*, *ABc*, *AbC*, *Abc*, *aBC*, *aBc*, *abC*, *abc*.

It will be observed that the number of kinds of chromosome sets present in a quartet of nuclei depends on the manner in which the chromosomes are oriented in mitoses *I* and *II*. For example, when all of the tetrads divide disjunctionally in *I* there are two types of sets in the quartet (Fig. 109). Also, when the tetrads divide equationally in *I* and the resulting dyads are then oriented similarly in the two mitotic figures in *II*, there are again two types (Fig. 110, *A*). If, however, after equational division in *I* the dyads are not similarly oriented in both figures in *II*, there are sets of four types in the quartet (Fig. 110, *B*). Four types also result when some of the tetrads divide disjunctionally in *I* while others do so in *II* (Fig. 110, *C*). Whether the number of types in a single quartet is two or four, however, is a minor matter, since the organism as a rule produces many quartets in which abundant opportunity is offered for the production of sets of all possible types.

A further point should be noted. The nuclei having *A* and *a* respectively will differ qualitatively according to the degree of difference between these chromosomes: if the original gonotokont nucleus was "heterozygous"[2] for this pair (*Aa*) the nuclei containing them will differ; whereas if it was "homozygous" (*AA* or *aa*), they will be alike, so far as this pair is concerned. The same holds for all of the pairs. In a completely homozygous individual meiosis might occur without producing any qualitative differences whatsoever among the nuclei of the quartet. The essential point to be borne in mind is that each nucleus of the quartet resulting from the meiotic divisions contains but one member of each homologous chromosome pair, rather than two as in the gonotokont nucleus. Although qualitative differences among the nuclei of the quartet usually obtain as the result of some heterozygosity in the original diploid complement, such differences are not always a necessary consequence of meiosis.

**Summary.**—*In a somatic mitosis each chromosome of the complement is split longitudinally, the halves passing to the daughter nuclei, which are therefore similar both to each other and to the mother nucleus: somatic mitosis is equational.*

*In the normal meiotic process each chromosome (or portion of a chromosome) is disjoined from its homologue in one mitosis, and is divided equationally in the other. Each of the four resulting nuclei contains a*

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[1] Demonstrated with pairs composed of dissimilar members in the orthopteran genera *Brachystola*, *Trimerotropis* (Carothers, 1913, 1917), and *Pseudotrimerotropis* (R. L. King, 1923).

[2] For these terms, see p. 371.

*chromosome set consisting of one member of each of the homologous pairs. The four nuclei differ qualitatively among themselves to the degree in which the various chromosomes differ from their respective homologues, and they furthermore differ from the original gonotokont nucleus in having only half as many chromosomes.*

*Meiosis involves essentially a change from the condition in which both members of a homologous pair of chromosomal units are present in the nucleus to the condition characterized by the presence of but one. This change may be accomplished for all of the units at either of the meiotic mitoses, or for some units at the first mitosis and for others at the second.*

## MODES OF MEIOSIS

In all cytology there is scarcely a question upon which there have been entertained so many opinions as upon that of the exact behavior of the chromosomes during the meiotic phase. Entirely aside from the theoretical interpretations placed upon meiosis, cytologists have yet failed to arrive at any universally accepted conclusion regarding all the structural changes which occur. This diversity of opinion is due in part to the complexity of the process and the difficulty of interpreting its various stages, some of which fail to stand out clearly in preparations made by our available methods. On the other hand, a great variety of organisms have been studied, and these undoubtedly differ considerably in the details of the meiotic process, so that agreement in all particulars is not to be expected. The attempt has too often been made to apply universally an interpretation founded upon a study of one or two organisms. Certain essential features of meiosis may be expected to show agreement in all organisms reproducing sexually, but it is evident that there is no full correspondence as regards the exact manner in which the essential changes are accomplished. In the following pages are given brief descriptions of a few representative interpretations advanced by various cytologists.[1]

Nearly all of the accounts of meiosis which have appeared in recent years have conformed in a general way to one or the other of two principal schemes, though they have varied greatly in detail. Each of the theories has been upheld by competent observers, and it is possible that both modes of meiosis may occur; but the fact that the same objects have been so differently described by the two schools suggests that interpretation is

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[1] No attempt can be made in a work of this scope to give a complete summary and classification of all the interpretations that have been put upon the meiotic phenomena. Only enough will be presented to afford a starting point for a study of this complex subject. For a review and criticism of all views expressed up to 1910, see Grégoire (1905, 1910). The student may follow the subject further in the recent general accounts of Agar (1920), Doncaster (1920), Tischler (1921–1922), McClung (1924), and Wilson (1925). Useful lists of works on somatic and meiotic mitosis in angiosperms are given by Picard (1913) and Ruys (1925).

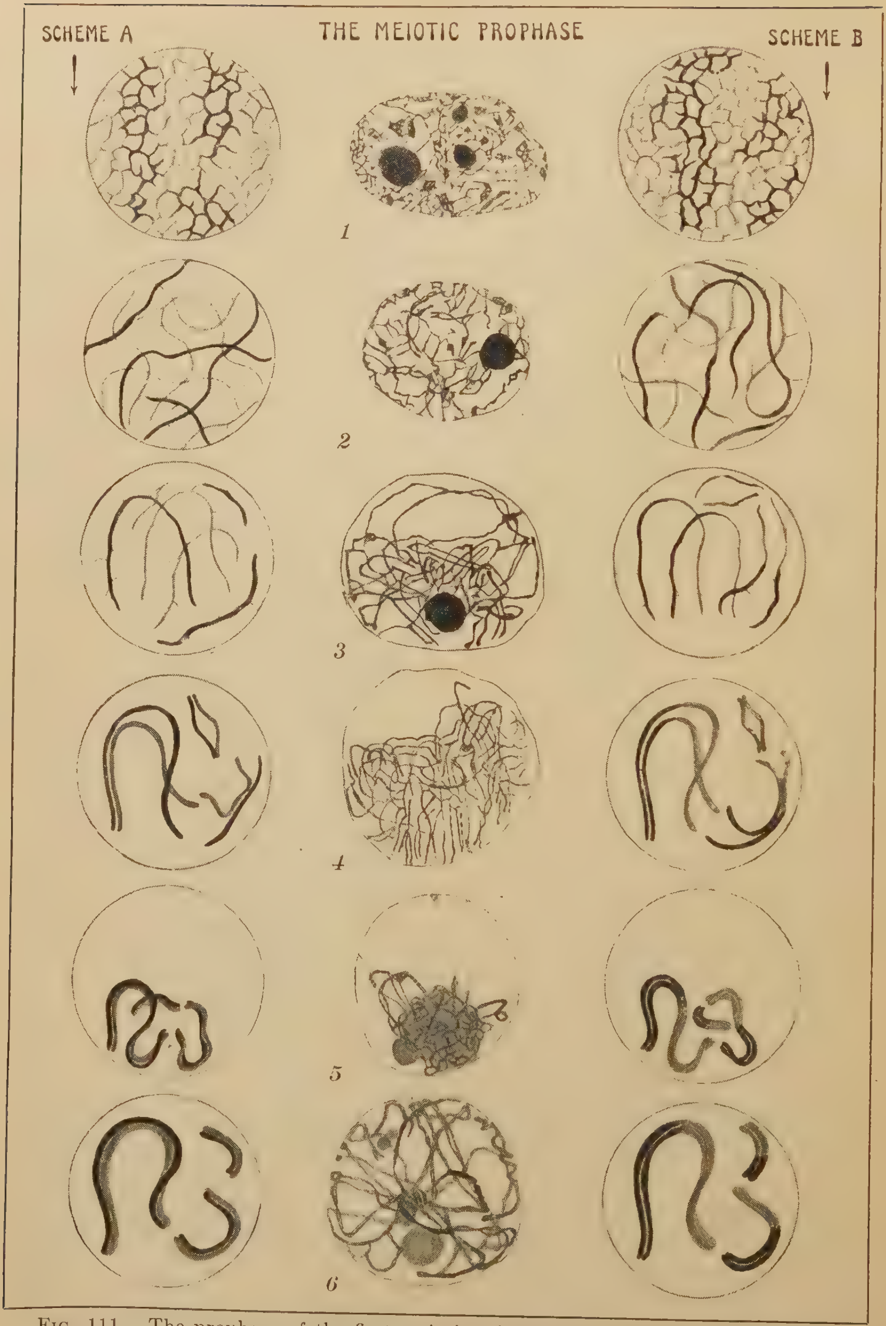
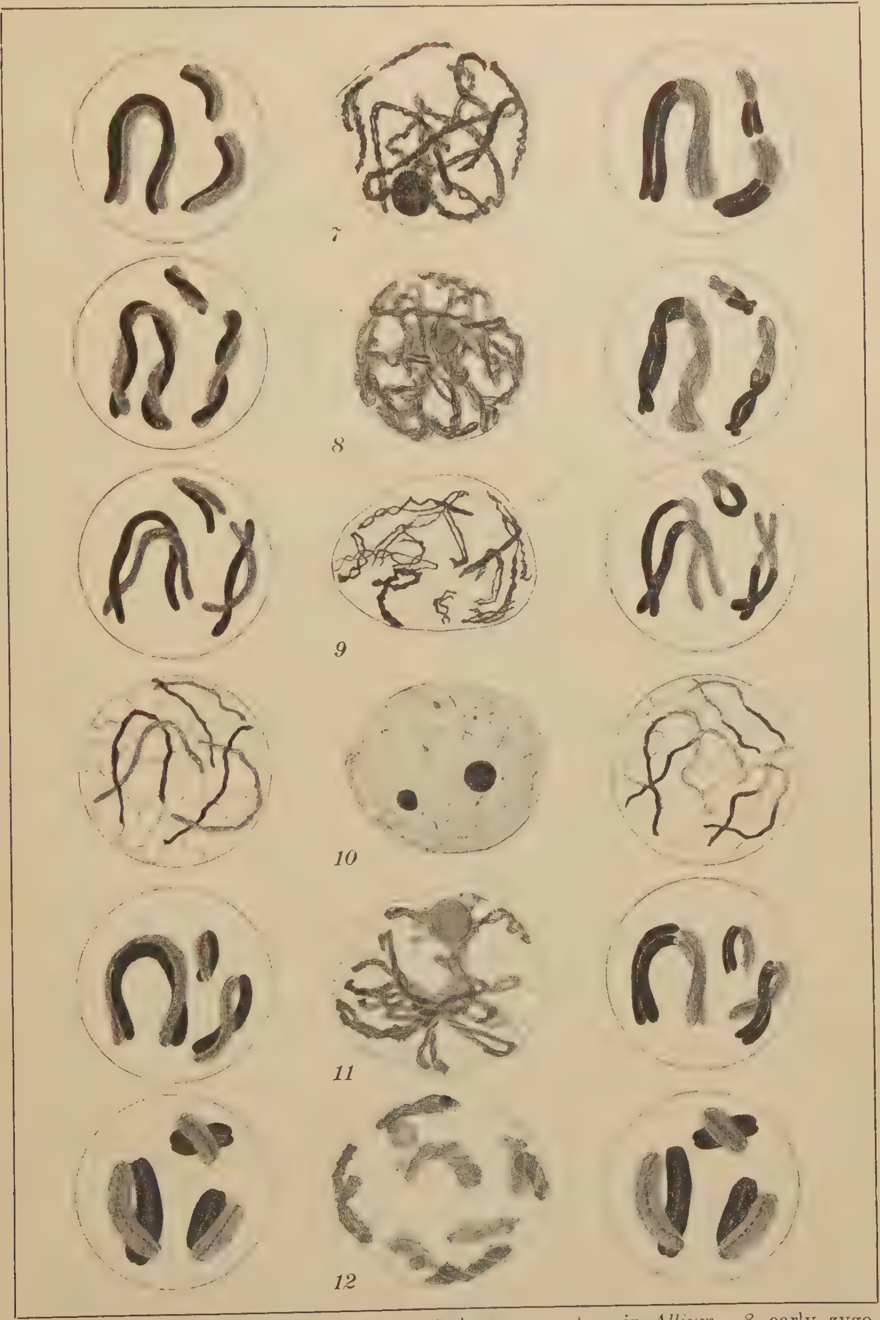


FIG. 111.—The prophase of the first meiotic mitosis up to the diakinesis stage, illustrated by typical figures taken from representative works on meiosis (middle column), together with diagrams showing the interpretation of each stage according to Scheme *A* (at left) and Scheme *B* (at right). The two members of each pair of homologous chromosomes are shown in black and gray. All figures in the middle column are of plant nuclei, with the exception of No. 10. In some cases stages 10 and 11 are lacking.



*1*, early sporocyte nucleus in *Lilium*. *2*, leptonema stage in *Allium*. *3*, early zygonema stage in *Allium*. *4*, zygonema stage in *Osmunda*. *5*, synizesis in *Lilium*. *6*, open spireme in *Lilium*. *7*, pachynema stage in *Lilium*. *8*, Strepsinema stage in *Lilium*. *9*, diplonema in *Allium*. *10*, diffuse stage in the oöcyte of *Scyllium*. *11*, second contraction in *Lilium*. *12*, diakinesis in *Lilium*.

(*1, 2, 3, and 4 after Grégoire*, 1907; *5, 6, 11 and 12 after Mottier*, 1907; *7 and 9 after Berghs*, 1904; *8 after Allen*, 1905; *10 after Maréchal*, 1907.)

largely responsible for the persistent diversity of opinion. The two interpretations differ chiefly with regard to the origin of the double chromosomes or tetrad chromosomes seen in the later prophase and metaphase of the first meiotic mitosis; beyond this point they are in general the same. The comparative diagram (Fig. 111) therefore illustrates the two interpretations up to the diakinesis stage; the subsequent stages appear in Fig. 112. The important question of synapsis will be discussed in greater detail later in the chapter. For convenience the two interpretations will be referred to as *Scheme A* and *Scheme B*.

**Scheme A.**—The first of the two main interpretations of meiosis came into prominence in 1900 and shortly thereafter, when von Winiwarter (1900), Grégoire (1904, 1907, 1909), A. and K. E. Schreiner (1904–1908), and Berghs (1904, 1905) applied it to the phenomena observed by them in several animals and plants. Its essential points are as follows:

At the beginning of the prophase of *I* the nuclear reticulum resolves itself into long slender threads (*leptotène* threads; *leptonema* stage).[1] These threads, particularly in animals, may be oriented with their ends directed toward the side of the nucleus on which the centrosome lies ("bouquet" stage).[2] In some cases they are said to form a more or less continuous spireme, which later breaks transversely into individual chromosomal threads. The leptotène threads very soon begin to conjugate in pairs side-by-side (parasynapsis). The association does not take place at all regions of the threads simultaneously: it begins at one or two points, commonly at one end, and gradually extends to all portions, so that when the process is only partially completed the threads may be closely paired at some points and widely divergent at others, presenting an appearance very unlike that of the halves of a longitudinally split chromosome in a somatic nucleus. This is known as the *zygonema*, *zygotène*, or *synaptène* stage. While the nucleus thus contains both thick double threads and thin single ones, it is said to be in the *amphitène* condition; this is especially well shown when the threads have the bouquet type of orientation. At about this time, often before the synaptic pairing is complete, the nucleus enlarges somewhat and the threads show a notable tendency to contract away from the nuclear membrane, especially under the influence of fixatives; in some cases the contraction seems to be wholly due to fixation. During this stage (*synizesis*) the association of the synaptic mates becomes very intimate. When the conjugated threads recover from synizesis they extend more or less uniformly throughout the nucleus (*open spireme*), and are seen to be considerably thickened (*pachynema; pachytène*). At this time the pachytène threads, notably in the animal spermatocyte, may have the form of loops with their ends directed toward the centrosome. If the line of synaptic union has been obscured by the closeness of the association during the pachynema stage it usually reappears later, the pairing members frequently diverging rather widely (*diplonema; diplotène*) and becoming more or less interlaced or twisted (*strepsinema; strepsitène*). In many cases they may then contract again into a loose knot with loops extending from it (*second contraction*). As the result of continued shortening and thickening the chromosomes eventually attain a compact form, and the various pairs (*gemini; bivalent chromosomes*), present in the haploid number, lie scattered throughout the nucleus (*diakinesis*). The two components of each geminus may now separate somewhat at one or both ends or at the middle, so that the various gemini appear in the form of **Y**s, **X**s, **V**s, and **O**s.

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[1] The terms *leptotène*, *synaptène*, *pachytène*, and *diplotène* were proposed by von Winiwarter (1900); *leptonema*, *zygotène*, *pachynema*, and *strepsinema* by Grégoire (1907); *amphitène* by Janssens (1905); *strepsitène* by Dixon (1901); *diakinesis* by Haecker (1897); *synapsis* by Moore (1896); *synizesis* by McClung (1905); and *meiosis* by Farmer and Moore (1905). The terms ending in *-tène* are ordinarily used as adjectives.

[2] Such a polarization of leptotène threads is often spoken of as the "thin bouquet," or "first bouquet," and that of pachytène threads as the "thick bouquet," or "second bouquet."

The foregoing description applies primarily to cases in which the synaptic mates show no clear evidence of longitudinal splits up to diakinesis. It has already been pointed out that in many cases—regularly in animals and apparently in some plants, though the latter point is disputed—the lines of separation for both meiotic mitoses are visible in the prophase of *I*, so that the chromosomes at diakinesis have the form of tetrads, each composed of two longitudinally split chromosomes. This increases in no inconsiderable measure the difficulty of interpreting the essential changes in meiosis. The splitting of each synaptic mate may apparently begin at various stages. In Fig. 111 it is indicated (by a dotted line) only in the late prophase, but in many animals it is known to be present during the zygonema stage or shortly thereafter, so that the threads throughout most of the prophase are quadruple rather than merely double (see Fig. 126, *Q*, *R*). Both Gelei (1921) and Janssens (1924), who have investigated this point with great care, observe the split first in the diplonema stage. Some observers think the threads may be split before they conjugate, even as early as the preceding telophase. Sometimes a split is seen only temporarily at some stage in the prophase.

In general, one may say that the tetrad chromosome is formed, according to *Scheme A*, as shown in Fig. 116, $A_1$-$C_1$. Two homologous chromosomes pair and split to form a tetrad of four chromatids (*D*), which may then open out along the synaptic plane or the splitting plane or both planes to form the various types of "rod," "cross," and "ring" tetrads observed during the later prophase and metaphase (*E*, *F*). Such a separation along the two planes at different regions may give very complicated figures, as in the compound ring tetrads of certain orthopterans

(Fig. 126, *U-X*). In many cases the tetrads condense into compact quadruple bodies before the end of the diakinesis stage.[1]

During the prophase of the first meiotic mitosis the cell and its nucleus usually become considerably enlarged. In case the growth continues well into the latter part of the prophase the chromosomes show a tendency to assume a finely divided form as in the metabolic stage. In the sporocytes of plants this alteration is comparatively slight: the synaptic threads, besides opening out more or less in the diplonema stage, may become noticeably irregular in outline, but usually they seem to pass into the diakinesis stage with little change other than shortening and thickening. In growing animal spermatocytes this modification of the diplotène threads is in some cases carried much further, so that a fairly distinct "diffuse stage" ensues. It is in the much more extensive "growth period" of the animal oöcyte, however, that it is most pronounced. At this time the cell increases enormously in size and undergoes most of the differentiation which is to characterize the egg; and as it does so the pachytène or diplotène threads become profoundly altered in appearance. They send out thready processes in all directions, and so assume an irregular brush-like form. The chromatic substance either may flow into the nucleolus, leaving the chromosome relatively unstainable and very difficult to observe, or, by loss of its staining capacity through chemical change, it may disappear from view completely.

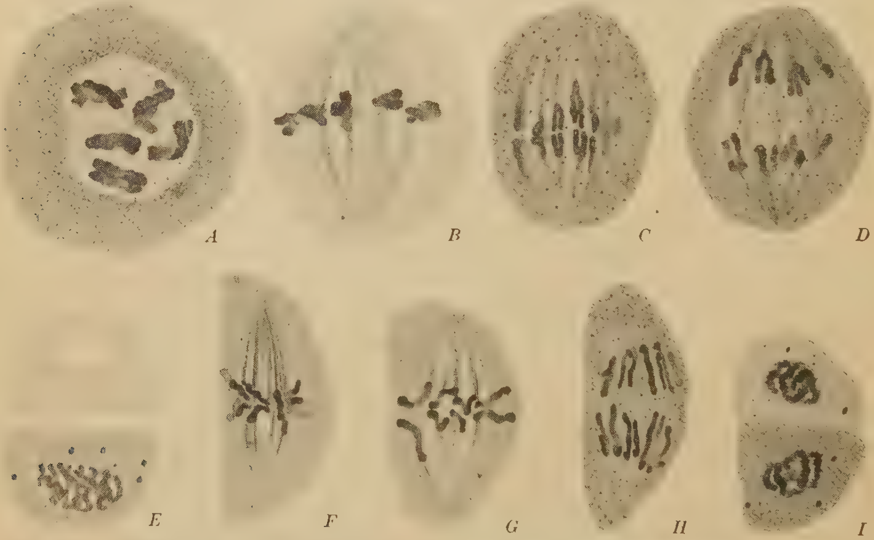

FIG. 112.—Meiosis in the microsporocyte of *Lilium* from diakinesis onward. *A–E*, first mitosis; note the split in the anaphase. *F–I*, second mitosis. (*After Grégoire*, 1899.)

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[1] For a fuller account of the formation of tetrads of various types and their manner of distribution in the meiotic divisions, see Wilson (1925).

As the growth period comes to an end, however, the original staining capacity returns, and the chromosomes again assume the compact form and pass into the diakinesis stage.

The distribution of the chromosomes by the two meiotic mitoses to the four resulting nuclei may now be considered. The diakinesis stage is terminated by the disappearance of the nuclear membrane, often after a marked shrinking about the chromosomes ("third contraction;" Fig. 113). The achromatic figure develops and the chromosomes take their places at its equator. The appearance of the metaphase stage of *I* is usually strikingly different from that of *II* or of a somatic mitosis; the chromosomes are usually short and swollen, and seem to be of a more fluid consistency than in other cells. As the anaphasic separation begins, the shapes assumed are particularly characteristic, owing largely to the location of the spindle fiber attachments (Figs. 112, 114, 117, 119).

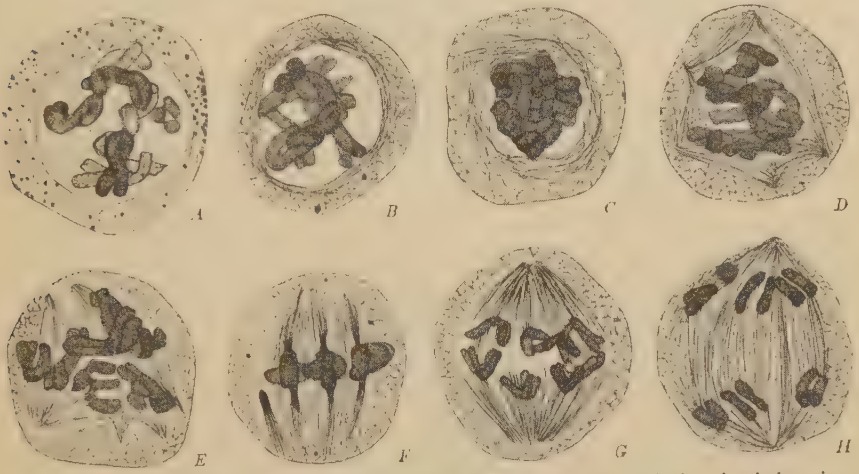

FIG. 113.—Late prophase, metaphase, and anaphase of first meiotic mitosis in microsporocyte of *Allium tricoccum*, showing especially the contraction of the nucleus at the end of the prophase. Note also the double nature of the chromosomes as they move apart in the anaphase. (*After Nothnagel*, 1916.)

If the bivalent chromosome shows no direct evidence of splits in its two components, or synaptic mates, these are separated in *I*, which is therefore disjunctional. As they pass toward the poles during the anaphase each of them reveals a longitudinal split; and, since the halves tend to open out along this split, any chromosome with terminal fiber attachment appears in the form of a simple V, while one with median attachment appears as a double V. The suddenness with which this split appears strongly suggests that it was present at an earlier stage, and that the chromosome was actually then a tetrad, although only double in appearance. There is even the possibility that the division in *I* may in some cases be along this invisible split and therefore equational, the doubleness suddenly appearing in the anaphase being due not to a split but to a widening out of synaptic mates. After reaching the poles the chromosomes may begin the reconstruction of daughter nuclei. As a rule this does not proceed far, since *I* is followed so closely by *II*. In some cases well-organized nuclei are formed (*interkinesis*); whereas in the animal egg there may be no reconstruction whatsoever, the daughter chromosomes of *I* at once taking their places in an achromatic figure newly formed for *II*. In *II* the chromosomes, if there has been an intervening interkinesis of any length, usually appear longer and more slender than in *I*. They are now separated along the line of division seen in the anaphase of *I*. When it is clear that it is the synaptic mates which disjoin in *I*, the division in *II* is consequently equational. If it were shown in any case that there is a division along an invisible split at *I*, then in such a case *II* would be disjunctional. A further complication is introduced by chiasmatypy, to which reference will later be made.

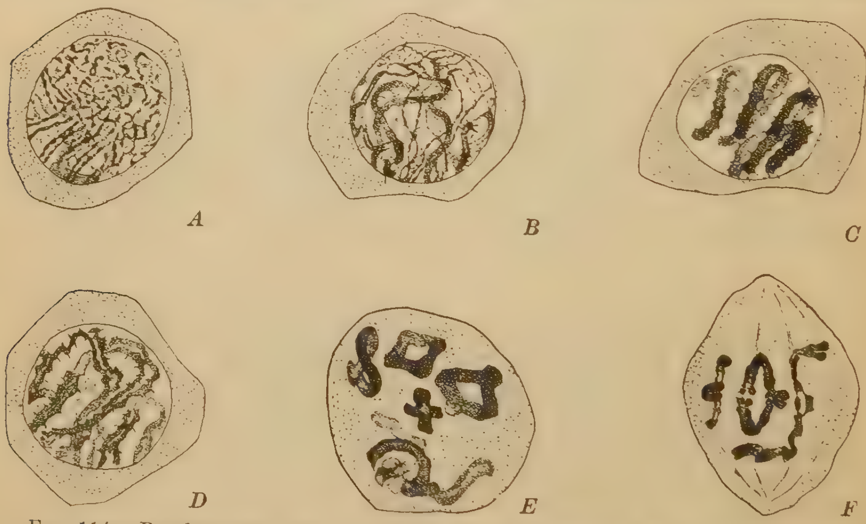

FIG. 114.—Prophase and metaphase of first meiotic mitosis in the spermatocyte of *Tomopteris onisciformis*. *A*, synapsis of leptotène threads beginning. *B*, synapsis complete in some pairs and only beginning in others; amphitène nucleus. *C*, pachynema stage. *D*, diplonema stage. *E*, diakinesis. *F*, metaphase. (*After A. and K. E. Schreiner*, 1905.)

In the case of organisms with plainly evident tetrad chromosomes, especially in the insects, the occurrence of the various possible modes of chromosome distribution in the two meiotic mitoses has been more clearly established. The four chromatids are commonly alike in appearance, so that it is very difficult to determine along which planes they are separated in *I* and *II*. In certain insects, however, it has been found (McClung, Carothers, Wenrich) that some of the chromosome pairs are *heteromorphic*, *i.e.*, the synaptic mates are unlike in size and form, which has made it possible to demonstrate that tetrads may divide along either plane in

*I.* In one case, for example, it has been shown that the same tetrad divides disjunctionally in *I* in half of the cells and equationally in the other half. Moreover, since the various tetrads are not all similarly oriented in the metaphase, some are divided disjunctionally and some equationally in each mitosis, so that disjunction is complete for the chromosome complement as a whole only after the close of *II* (Fig. 110, *C*). As McClung (1924) points out, such facts show that formal theories of "prereduction" and "postreduction" have little significance, and serve to emphasize the essential unity of the entire meiotic process.[1]

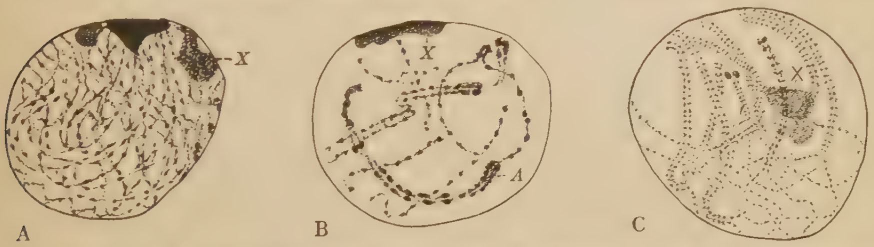

Fig. 115.—*A*, leptonema stage in *Phrynotettix; X*, sex-chromosome. *B*, parasynapsis of chromosome pair "A" in *Phrynotettix*. *C*, parasynapsis in *Trimerotropis*. (*After Wenrich*, 1916.)

**Scheme B.**—This interpretation of meiosis was first made by Farmer and Moore (1903, 1905). Since many features common to both interpretations were included in the account of *Scheme A*, the description of *Scheme B* may be briefer. The essential points may be stated as follows:

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[1] Among the works in which *Scheme A* in one form or another has been described may be mentioned the following:

In animals: von Winiwarter (1900) on the rabbit and man; Maréchal (1904, 1905, 1907) on tunicates, selachians, teleosts, and *Amphioxus;* A. and K. E. Schreiner (1904, 1905, 1906, 1908) on *Tomopteris, Ophryotrocha, Zoögonus, Enteroxenos, Myxine, Salamandra,* and *Spinax;* Lerat (1905) on *Cyclops;* Grégoire (1909) on *Zoögonus;* Janssens (1905, 1909, 1924) on *Batracoseps, Stethophyma,* and *Chorthippus;* Schleip (1906, 1907) on *Planaria;* Debaisieux (1909) on *Dytiscus;* Montgomery (1911) on *Euschistus;* Kornhauser (1914, 1915) on *Hersilia* and *Enchenopa;* Wenrich (1916, 1917) on *Phrynotettix* and *Chorthippus;* Robertson (1916, 1920) on insects; Mohr (1915) on *Locusta;* de Baehr (1909, 1912, 1913, 1920*ab*) on *Aphis* and *Saccocirrus;* Dingler (1910) on *Dicrocœlium;* Wilson (1912) on insects; Bordás (1921) and Gelei (1921, 1922) on *Dendrocœlum;* Bouin (1922, 1925) on *Scolopendra;* Agar (1923) on marsupials.

In plants: Grégoire (1904, 1907) on *Lilium, Allium,* and *Osmunda;* Berghs (1904, 1905) on *Allium, Drosera,* and *Helleborus;* Rosenberg (1905, 1907, 1908, 1909) on *Drosera* and Compositæ; C. E. Allen (1905*bc*) on *Lilium* and *Coleochæte;* J. B. Overton (1905, 1909) on *Thalictrum, Calycanthus,* and *Richardia;* Tischler (1906) on *Ribes;* Strasburger (1905, 1907, 1908, 1909*b*) on *Lilium, Galtonia,* etc.; Miyake (1905*a*) on *Lilium, Funkia, Iris, Allium, Tradescantia,* and *Galtonia;* Lagerberg (1906, 1909) on *Adoxa;* Yamanouchi (1906, 1908*a*, 1910) on *Polysiphonia. Nephrodium,* and *Osmunda;* Martins Mano (1909) on *Funkia;* Lundegårdh (1909, 1914) on *Trollius;* Frisendahl (1912) on *Myricaria;* Sakamura (1914) on *Vicia;* de Litardière (1912) on *Polypodium;* Schwemmle (1924) on *Epilobium;* Komai (1920) on *Squilla.*

In the early prophase of *I* the reticulum resolves itself into slender threads which pass into the synizesis contraction. When they later loosen up the threads are seen to have the form of a more or less continuous "open spireme," which is double. This doubleness is explained by the advocates of *Scheme B* as the result of a true longitudinal splitting, and not of a synaptic pairing as in *Scheme A*. In earlier accounts the

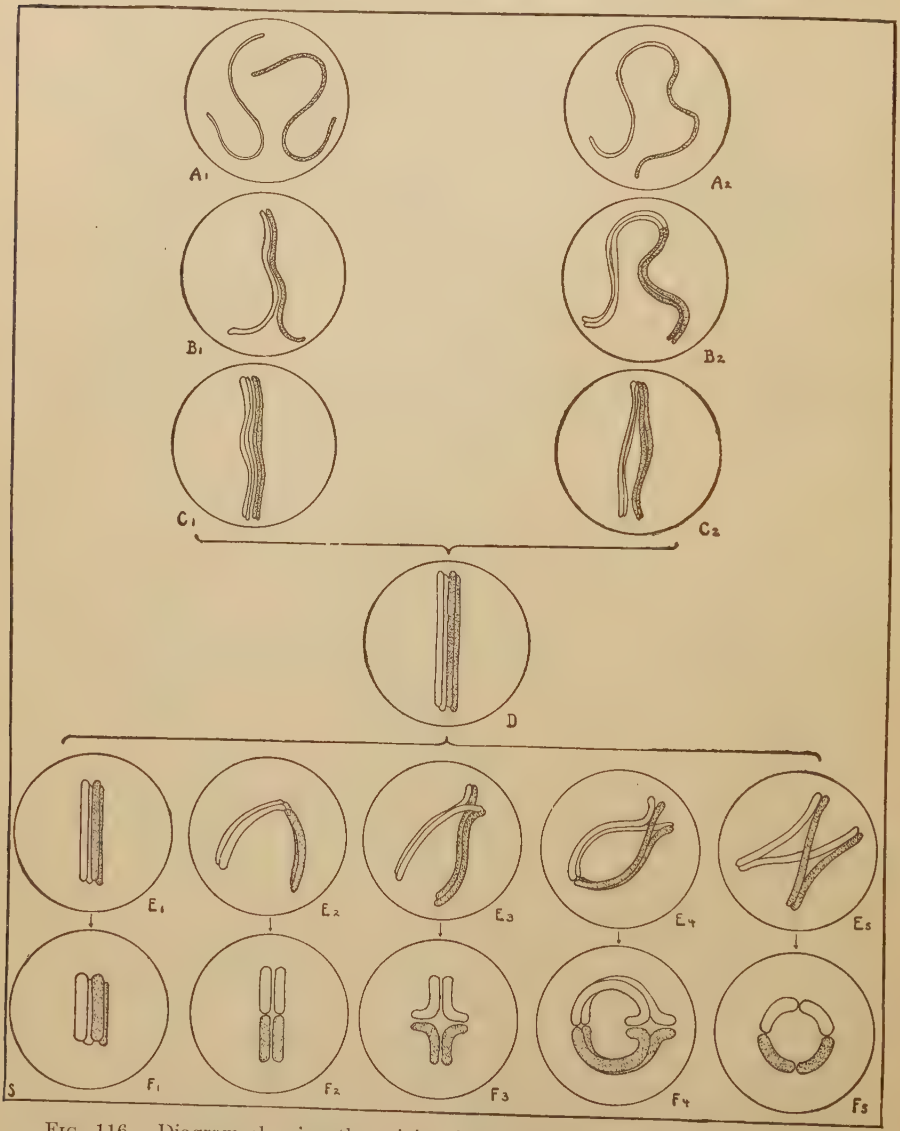

FIG. 116.—Diagram showing the origin of the tetrad chromosome (*D*) according to *Scheme A* ($A_1$–$C_1$) and *Scheme B* ($A_2$–$C_2$), and the further transformation of this chromosome into tetrads of five types ($F_1$–$F_5$).

split was thought to arise during or immediately after synizesis, but the threads have subsequently been more carefully studied in the stages prior to synizesis, and the lateral pairing described by the advocates of *Scheme A* has been found. This pairing, however, is not regarded as a synaptic conjugation, but rather as the reassociation of the halves of chromosomes which have been split in the preceding telophase (Digby, Fraser, Nothnagel, Santos). The double spireme now becomes thickened (pachynema) and twisted (strepsinema), and during the "second contraction" it is thrown into loops. The loops then break apart from one another through a segmentation of the spireme; each loop is composed of two split chromosomes arranged end-to-end (telosynapsis). Chromosome conjugation therefore occurred when the spireme was formed. The two members of each pair are brought to a side-by-side position by the looping at the second contraction, and they may or may not remain closely connected at the original point of conjugation. The bivalent chromosomes, with the synaptic mates now side-by-side, become shortened and thickened and pass into the diakinesis stage. The early split in each of the synaptic mates becomes obscured during the middle portion of the prophase and does not reappear until later. In case it remains obscured through the metaphase, as stated in most of the accounts, mitosis *I* divides the chromosomes disjunctionally, *II* being equational along the early split which reappears in the anaphase of *I*. If the split reappears before the metaphase of *I*, tetrads are present, with the various possibilities of distribution pointed out under *Scheme A*.

Because of the frequently described folding of each chromosome upon its synaptic mate this interpretation was for some time known as the "folding theory." But the folding and the telosynaptic arrangement are not the principal features; in several accounts both the continuity of the spireme and the folding are said to be imperfect or absent (*e.g.*, Lawson, 1912). The essential point is the interpretation of the doubleness of the early prophasic threads as due to splitting rather than to synapsis. The lateral arrangement of synaptic mates arises much later in the prophase.[1]

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[1] Among the works in which *Scheme B* in some form is described may be mentioned the following:

In animals: Farmer and Moore (1905) on *Periplaneta* and elasmobranchs; Montgomery (1903–1910) on Hemiptera and amphibia; Griggs (1906) on *Ascaris;* H. S. Davis (1908) on insects; Nakahara (1920) on *Perla;* Jordan (1911) on *Didelphys;* Wassermann (1913, 1922) on *Zoögonus* and *Tomopteris;* Brunelli (1911) on *Tryxalis.*

In plants: Farmer and Moore (1903, 1905) on *Lilium, Osmunda, Psilotum,* and *Aneura;* Farmer and Shove (1905) on *Tradescantia;* Farmer and Digby (1910) on *Galtonia;* Mottier (1907, 1909, 1914) on *Lilium, Acer, Allium, Podophyllum, Tradescantia,* and *Staphylea;* Schaffner (1906, 1909) on *Agave;* Digby (1910, 1912, 1914, 1919) on *Galtonia, Primula, Crepis,* and *Osmunda;* Fraser (1914) on *Vicia;* Nothnagel (1916) on *Allium;* Gates (1920*a*) and Gates and Rees (1921) on *Lactuca;* Osawa (1920) on *Morus;* O'Neal (1920) on *Datura;* Santos (1923, 1924) on *Elodea.*

**Discussion of Schemes A and B.**—The principal points of the two foregoing interpretations of meiosis may be summarized as follows: According to *Scheme A* the leptotène threads, each representing an entire chromosome, pair laterally; the double threads so formed shorten and thicken, and directly become the double chromosomes or gemini seen at diakinesis. In case each of the synaptic mates splits at any time prior to the anaphase of *I*, the chromosomes may appear as tetrads rather than merely double. According to *Scheme B* the pairing leptotène threads are reassociating halves of chromosomes previously split; the double threads formed by the reassociation shorten and thicken, and the double chromosomes seen at diakinesis arise by a lateral approximation of such threads late in the prophase, rather than directly as in *Scheme A*. If the original doubleness (split) becomes obscured, the chromosomes in the diakinesis and metaphase stages appear as simple gemini; if it remains evident or reappears before the anaphase they have

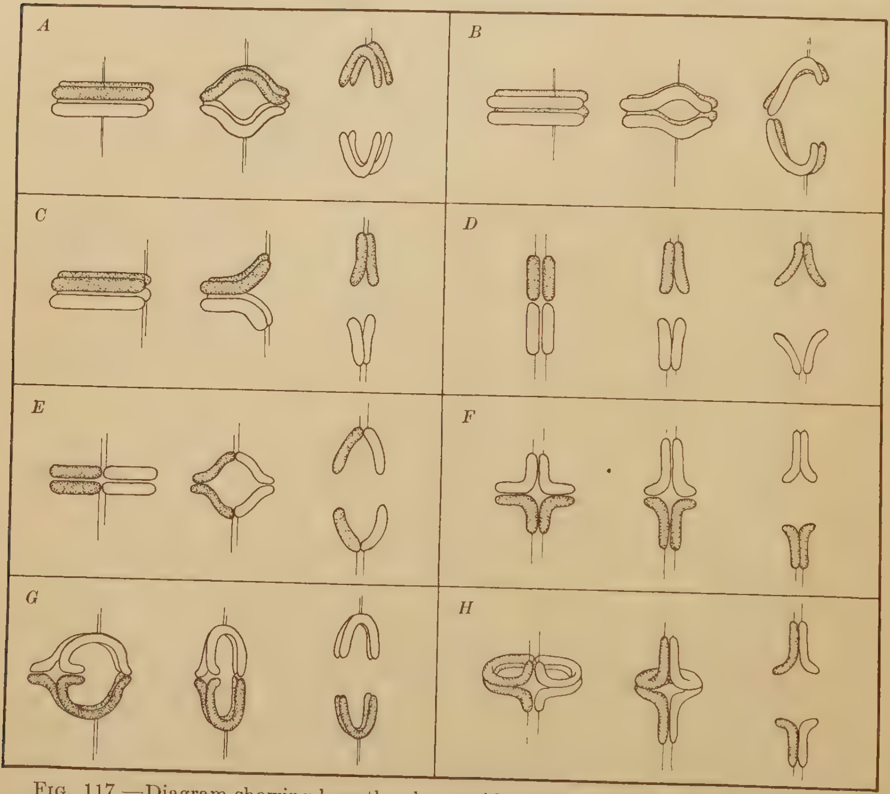

FIG. 117.—Diagram showing how the chromatids of tetrads of various types and with various kinds of spindle attachment may be distributed in the first meiotic mitosis. In each case the two chromatids passing to one pole in *I* are separated in *II*. *A*, *C*, *D*, *F*, and *G* show prereduction; *B*, *E*, and *H* show equational separation in *I*, which will be followed by postreduction.

the form of tetrads. After both modes of bivalent chromosome development, the same variety of distributions may occur in the two meiotic divisions, giving, in general, the same result in the four nuclei. In connection with the rôle of the chromosomes in heredity, however, the distinction is a very significant one, as will later be shown. The discussion of this matter centers in one primary question: is the pairing of leptotène threads in the early prophase of the first mitosis a parasynapsis of homologous chromosomes (*Schema A*) or the closing of a longitudinal split (*Scheme B*)?

The theory of a closing split has been advocated by several botanists (Digby and others) who have interpreted somatic splitting as a telophasic process, the resulting double threads persisting through to the following prophase. Hence they homologize the doubleness of the first meiotic prophase with that of a somatic prophase, the only conspicuous difference being the relatively wide separation of the longitudinal halves in the former case. Reference has been made to the inadequacy of the evidence for telophasic splitting in somatic cells (p. 152); such evidence, therefore, can scarcely be regarded as strongly supporting the view that two pairing leptotène threads are halves of a chromosome split in the premeiotic telophase. It is not impossible, however, that the premeiotic telophase may differ in certain respects from the ordinary somatic telophase; further information on this point is much needed.

The foregoing view involving telophasic splitting should not be confused with another advanced by certain zoölogists. Robertson (1920), McClung (1924), and others have been led to believe that the leptotène threads which undergo parasynapsis may in some cases be split as early as the preceding telophase. Janssens (1924) also views this as a possibility, though discovering no very direct evidence for it. According to this interpretation, therefore, the two pairing leptotène threads are split chromosomes undergoing parasynapsis, and not the reassociating halves of one split chromosome as in *Scheme B*.

Decisive evidence on the question of the relationship of the pairing leptotène threads has been difficult to obtain in plants because the threads are long and irregularly intermingled, making their enumeration or individual identification next to impossible. Much more favorable material has been found among animals, especially the insects. In the Orthoptera, for example, Wenrich (1916) has shown that the individual chromosomes can be distinguished by the form and arrangement of their chromomeres from the spermatogonia through to the spermatids. During the prophase of *I* pairs of chromosomes with corresponding chromomere patterns conjugate parasynaptically, comparison with the spermatogonia showing that these are whole chromosomes and not longitudinal halves (Figs. 65, 115). Some chromosome pairs, moreover, are heteromorphic, the two members showing a constant difference in length, which would not be true of the halves of a split chromosome. An especially clear case has been found in a flatworm, *Dendrocœlum lacteum*, by Bordás (1921) and by Gelei (1921) (Fig. 118). Here there are seven pairs of somatic chromosomes, distinguished by individual size differences. In the early prophase of *I* the 14 chromosomes all appear as distinct leptotène threads and assume the bouquet type of orientation. The two members of each pair, which may not at first lie near each other, move together and undergo parasynaptic union, all stages of which may be followed in each pair. In this way there arise seven thick loops, which shorten to form the gemini of diakinesis. Further evidence that the pairing of leptotène threads is a parasynapsis of homologues has been discovered by Janssens (1924) in the insect *Stethophyma grossum*, in which each reticulate chromosome can be seen to give rise to but one leptotène thread, and in which the figures are not complicated by looping. The important work of Janssens will be further considered later in the chapter.

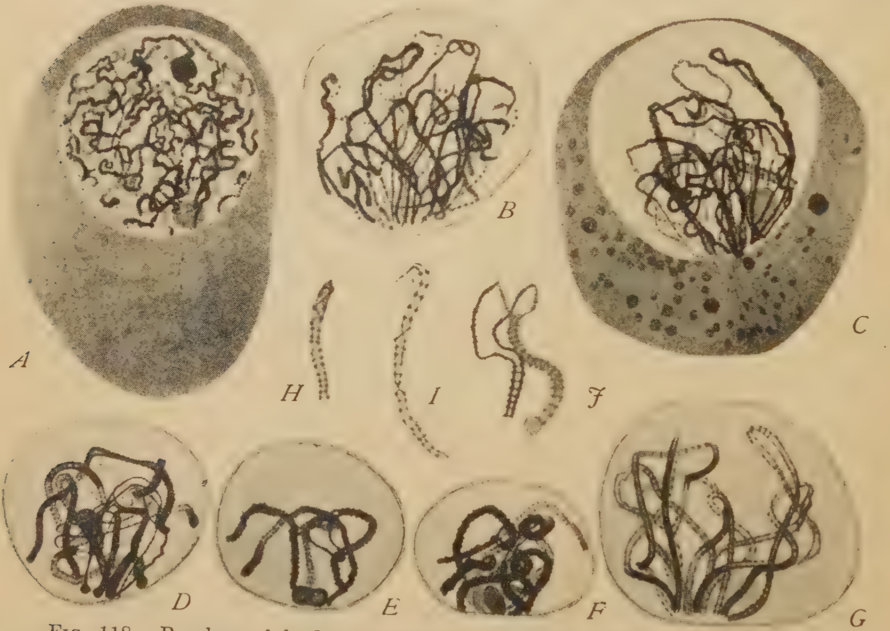

Fig. 118.—Prophase of the first meiotic mitosis up to the pachynema stage in the oöcyte of *Dendrocœlum lacteum*. *A*, young oöcyte with spiremes. *B*, leptotène bouquet, 14 loops. *C*, parasynapsis in progress; note orientation of threads toward centriole. *D*, later stage of parasynapsis. *E*, two threads prevented from conjugating in middle portion by other threads caught between them; an exceptional case. *F*, parasynapsis nearly completed. *G*, pachytène bouquet, 7 loops. *H*, the crossing of strands between successive chromomeres in pachytène thread. *I*, twisting of bivalent thread between successive chromomeres. *J*, single chromosome pair with synapsis only partially completed. (*After Gelei*, 1921.)

It may be concluded from the above considerations that the synaptic union of homologous chromosomes in the form of leptotène threads

(*Scheme A*) has been demonstrated in a number of instances, and it seems reasonable to infer that a similar interpretation is to be put upon many of the other cases in which the succession of stages cannot be so clearly observed. Equally cogent evidence for *Scheme B* has not been produced, though certain special cases of meiosis show many of the features of this scheme, as will be seen further on. Some have suggested that one scheme may have been derived from the other in some way, perhaps as follows: simple telosynapsis; telosynapsis followed by a folding to the parasynaptic position; parasynapsis with no previous telosynapsis or folding. Such a theory is suggestive, but too much weight should not be placed upon it.

**Are Tetrad Chromosomes Universal?**—In our descriptions of the process of meiosis, the chromosomes of the first meiotic prophase and metaphase have been treated as bivalent structures which may appear either double, as in most plants, or quadruple, as in most animals, this unlikeness being due to a difference in the time at which the synaptic mates reveal a split. In this way our descriptions have been kept in accord with what has so far been established cytologically. Although one is by no means warranted as yet in saying that all meiotic chromosomes are tetrads, there is much to suggest that the gemini in plants are structurally quadruple. For instance, as the synaptic mates disjoin in the anaphase of *I* they reveal a longitudinal split with startling suddenness, often before they have lost contact with each other (Fig. 119). That this split actually originates at this moment seems scarcely possible, especially in the light of the significance usually attached to the thread-like form of the chromosomes in somatic prophases (p. 166). It seems more likely that the synaptic mates actually have a split which is for some reason invisible until the anaphasic movement begins. The split in somatic chromosomes and the synaptic line in meiotic chromosomes are known to pass through periods of relative obscurity in many cases; but why the split, if actually present, should be so persistently invisible in the meiotic chromosomes of plants and visible in those of animals is not easy to explain.

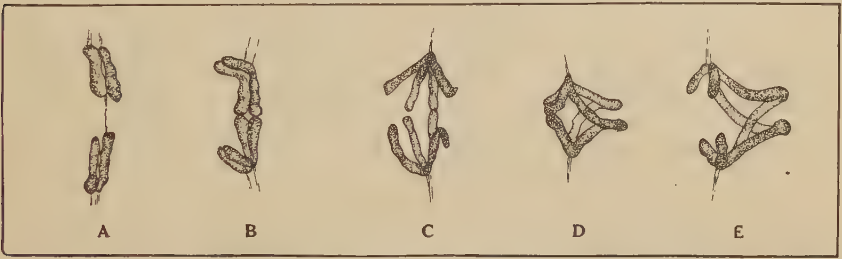

FIG. 119.—Plant chromosomes in the early anaphase of the first meiotic mitosis, showing tetrad nature. (*A after Allen; B after Mottier; C–E after Strasburger.*)

In the literature there are descriptions of tetrad chromosomes in several plants,[1] but what has recently been ascertained regarding chromosome constrictions renders any evaluation of these reports rather uncertain. That one of the supposed division planes in such tetrads is often neither a synaptic line nor a split, but a constriction in the chromosomes, seems evident. Thus Sakamura (1920), who has made a study of constrictions in both normal and chloralized cells, interprets reported plant tetrads as pairs of constricted chromosomes. This is also the conclusion of Chambers and Sands (1923) regarding living *Tradescantia* chromosomes. Sakamura denies that the quadripartite condition has anything to do with meiosis in such cases. He likewise accounts for the telosynaptic rod tetrads described by several investigators of meiosis in animals, holding that they represent two constricted chromosomes conjugated parasynaptically rather than two split ones placed end-to-end. In support of this contention he cites the following observations: such "tetrads" are seen not only in the oöcytes and spermatocytes, but also in oögonia, spermatogonia, and somatic cells; the supposed telosynaptically conjugated members are often very unequal in size; such tetrads are sometimes divided in the transverse plane at neither meiotic mitosis; not only quadruple, but also six- and eight-parted chromosomes are often observed, even in the same cell, and these are plainly due to the presence of additional accentuated constrictions. There are several cases in animals in which supposed synaptic points have turned out to be constrictions with no relation to meiosis. From these considerations it seems evident that much of the evidence heretofore offered in support of the view that the meiotic chromosomes of plants are tetrads is of questionable value.

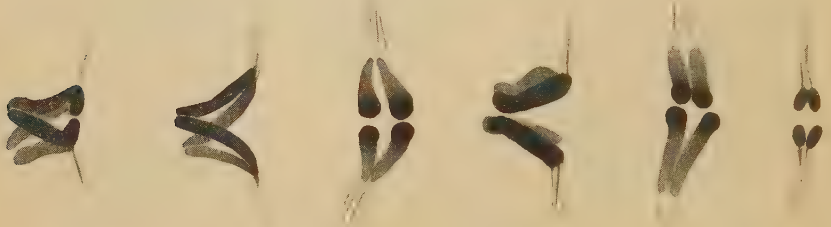

FIG. 120.—Tetrad chromosomes in the first meiotic mitosis in the microsporocyte of *Gasteria verrucosa*. (*Figure kindly furnished by Dr. W. R. Taylor.*)

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[1] *Fossombronia* (Farmer, 1895); *Pallavicinia* (Moore, 1905); *Sphagnum*(Melin, 1915); *Chiloscyphus* (Florin, 1918*a*); *Equisetum* (Osterhout, 1897); *Pteris* (Calkins, 1897); *Arisæma* (Atkinson, 1899); *Tricyrtis* (Ikeda, 1902); *Spinacia* (Stomps, 1911); *Primula* (Digby, 1912); *Lopezia* (Täckholm, 1914); *Thalicturm, Calycanthus*, and *Richardia* (J. B. Overton, 1909).

On the other hand, the newer evidence brought forward by W. R. Taylor in his studies on the chromosomes of *Gasteria* affords strong confirmation of the suspicion that the gemini of plants really have a quadruple constitution (Fig. 120). Not only in the anaphase of *I*, but also in the metaphase, the chromosomes are very clearly tetrads, which must mean that the split in each synaptic mate has developed at some earlier stage. If, as these observations suggest, refined methods are to demonstrate the fact that what are fundamentally tetrads characterize meiosis in plants as well as in animals, although the split tends to remain obscure in the former case, we shall have the advantage of being able to apply a single general description to meiosis in both kingdoms.

**Œnothera.**—In the genus *Œnothera* there has been found a very peculiar type of meiosis, which is of special interest in view of the prominent place occupied by this genus in the literature of genetics.[1] According to the accounts of Gates, Davis, and Cleland, the chromatic threads appearing in the prophase of *I* show neither a lateral pairing nor a longitudinal split, but take the form of one or more chains or rings of chromosomes, which have often been likened to strings of sausages. The various chromosomes apparently have a very definite space relationship in these chains or rings. In *Œ. franciscana*, for example, there is one ring of four and five other rings of two each, making fourteen chromosomes in all (Fig. 121, *A*). In *Œ. muricata* all fourteen occur in one ring, and in *Œ. franciscana sulphurea* there is one ring of twelve and one of two (Fig. 121, *E*). The chromosomes of the various species and varieties thus show a varying tendency to form definite synaptic pairs (the rings of two), and they differ correspondingly in their subsequent behavior.

In *Œ. grandiflora* (Davis) and *Œ. franciscana* (Cleland) the longer chains or rings break up into telosynaptic pairs, which undergo a folding (as in *Scheme B*), pass to the equator of the spindle figure, and disjoin regularly in *I*. The split for *II* appears in the anaphase of *I* in *grandiflora*, according to Davis, but in *franciscana* Cleland cannot make it out until late in interkinesis. The chromosomes divide equationally in *II*.

In contrast to *grandiflora* and *franciscana*, a number of other investigated species and varieties show little or no tendency to form separate synaptic pairs, and exhibit considerable irregularity in the meiotic mitoses. In *rubrinervis* Gates reported such an irregularity. In *Lamarckiana* and *gigas* Davis found no actual synapsis or diakinesis, and considerable irregularity in the distribution of the chromosomes in *I*. Also in *biennis*, *biennis sulphurea*, and *muricata* Cleland reports that no separate pairs are formed, all of the chromosomes forming one or two chains of more than two each. Cleland has described an arrangement of these chains in the metaphase of *I* whereby contiguous chromosomes pass to opposite poles and alternate ones to the same pole, giving thus the effect of disjunction in spite of the lack of synaptic pairing other than that in the common chain, assuming that contiguous chromosomes are homologous. Unfortunately, there are no size differences among the chromosomes which will serve to determine this last point directly. In *biennis* S. H. Emerson (1924*a*) reports that the distribution is quite irregular, rather than regularly alternate as found by Cleland.

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[1] Chromosome behavior in *Œnothera* has been studied chiefly by Gates (1908, 1909, 1911), Geerts (1907–1911), B. M. Davis (1909, 1910, 1911), Lutz (1912, 1916, 1917), Cleland (1922, 1923, 1924, 1925), S. H. Emerson (1924), Schwemmle (1924), Boedyn (1924), Valcanover (1925). See the review by Oehlkers (1924).

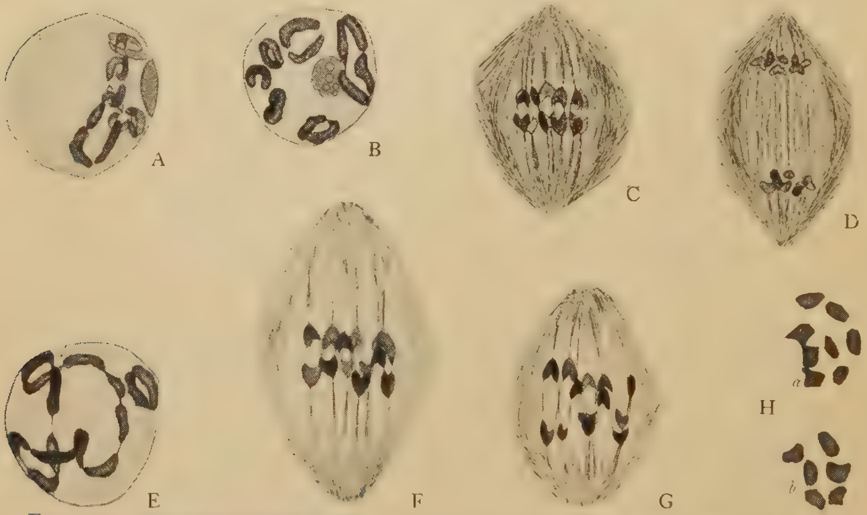

Fig. 121.—Stages in meiosis in the microsporocytes of *Œnothera*. *A–D*, *Œ. franciscana:* *A*, prophase showing a ring of 4, and 5 pairs. *B*, diakinesis, after separation of pairs from the ring. *C*, metaphase of *I*. *D*, anaphase, showing regular distribution. *E–H*, *Œ. franciscana sulphurea:* *E*, prophase showing ring of 12 and one pair. *F*, alternate chromosomes in the ring of 12 passing to the same pole in anaphase; single pair not shown. *G*, later stage; all chromosomes shown. *H*, anaphase of division *II*, with 8 chromosomes in one figure and 6 in the other; this is due to an occasional irregularity of distribution in *I*. (*After Cleland*, 1922, 1924.)

Of considerable theoretical interest is the fact that the species with regular chromosome behavior in meiosis are genetically stable (*grandiflora; franciscana*), whereas those characterized by irregularities are relatively unstable, forming mutants rather freely. Cleland suspects that the formation of chains of more than two chromosomes rather than regular synaptic pairing may be due to hybridity. Håkansson (1925) finds support for this idea in the nearly related genus *Godetia*. In *G. amœna* and *G. Whitneyi*, which, like many *Œnotheræ*, have seven pairs of chromosomes, the tendency to form such chains is very slight or absent, whereas in hybrids between the two species it is very pronounced. The relation of meiotic aberrations to hybridity is to be discussed at length in Chapter XVII.

**Further Cases and Interpretations.**—In addition to the modes of meiotic chromosome behavior outlined in the foregoing pages, the literature contains descriptions of a number of others. In many instances the interpretations involved are of questionable validity, but one illustrative example of a less doubtful nature may be mentioned.

A. Schellenberg (1911) describes a modification of *Scheme B* with tetrads in the parasitic flatworm, *Fasciola hepatica* (Fig. 122). The karyotin in the prophase of *I* takes the form of a long slender filament which splits longitudinally soon after synizesis. This double thread then breaks into the haploid number of pieces, each representing two chromosomes end-to-end; these have the form of loops with a definite orientation ("first bouquet stage"). Each piece breaks again, giving the diploid number of split chromosomes, which again assume the form of oriented loops ("second bouquet stage"). The halves twist tightly about each other, shorten to form the double bodies seen at diakinesis in the diploid rather than the haploid number, and then conjugate to form the haploid number of tetrad chromosomes. The conjugated members (each split) disjoin at the first mitosis, and in the second mitosis the separation is along the line of the original split. According to this interpretation, therefore, the doubleness of the early prophase

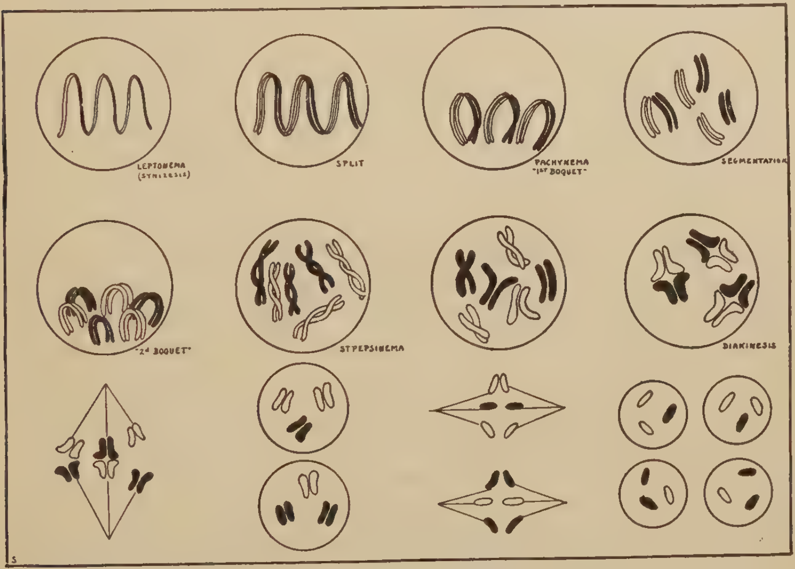

FIG. 122.—Meiosis in *Fasciola hepatica*, according to Schellenberg (1911).

of *I* is due to a split, as in *Scheme B*, but the chromosomes arranged end-to-end soon become separated and do not pair again until diakinesis.

The tetrad chromosome of *Ascaris megalocephala*, the threadworm which has been the subject of so many cytological studies, was once thought to be exceptional in being formed by two longitudinal fissions of a primary rod, which seemed to give no opportunity for true disjunction. But it has since been shown that it arises, as in other organisms, by the conjugation of two split chromosomes (Sabaschnikoff, 1897; Tretjakoff, 1904; Griggs, 1906). In oögenesis Tretjakoff describes parasynapsis followed by postreduction. In *Ascaris canis* (Marcus, 1906; Walton, 1918) each of the four chromatids shows a transverse constriction, the tetrad in the first mitosis having an eight-parted form.

**Researches on Living Cells.**—The large literature pertaining to meiosis deals almost wholly with fixed material, but a beginning has been made in the investigation of the meiotic phase in living cells. A case in point is the insect spermatocyte studied by Chambers (1924, 1925). The living nucleus of the spermatocyte resembles nuclei of other cells in being optically homogeneous, except for nucleoli. In the early part of the growth period slight injury, such as puncturing the nuclear membrane with a needle, causes the almost immediate appearance of granular filaments, which seem to be hyaline cores with investing clumps of granules. Ten minutes later the filaments are much thicker, and after another ten minutes they are short rod-like bodies. Nuclei punctured at a somewhat later stage show rings and crosses almost at once; sometimes these are visible before the puncture is made, becoming more clearly visible afterward. Such structures are not actually formed anew as artifacts, but their relative invisibility seems rather to be due to the similarity of their refractive index to that of the nuclear fluid in which they lie, the injury in some way causing an alteration of their optical properties.

Thus it is found that mechanical injury to the spermatocyte nucleus at various stages during the prophase of *I* brings into view a series of structures which have been slowly developing, and accelerates their further changes into fully formed chromosomes. The structures and changes so observed, moreover, are essentially the same as those observed in material treated by the acetocarmine process and the older methods of fixation.

Meiosis has been observed also in the living cells of an orchid, *Gymnadenia conopea*, by Chodat (1924). In the megasporocyte, which is here surrounded by only one layer of transparent nucellar cells, the nucleus is seen by oblique illumination to possess a reticulate structure. Leptotène threads, pachytène threads, and gemini are successively observed. In the metaphase the eight gemini become arranged at the equator of a hyaline achromatic figure, after which their disjunction and passage to the two poles can be followed. So far as these observations go, therefore, they are in harmony with accounts of meiosis based on fixed material, and serve to strengthen our confidence in those accounts, at least so far as the general behavior of the chromosomes is concerned.

## SYNAPSIS

Synapsis, or chromosome conjugation, which has been seen to play such a prominent rôle in meiosis, is one of the most significant features of chromosome behavior from the standpoint of the nuclear theory of heredity. Closer examination should therefore be made of certain points which have already been touched upon.

**The Stage at Which Synapsis Occurs.**—In the great majority of observed cases synapsis takes place during the prophase of the first meiotic division. Since the chromatic threads at a relatively early stage during the prophase usually show a tendency to contract into a knot and immediately afterward appear clearly double, it was suggested (Moore, 1896) that the contraction is an important factor in bringing about conjugation, and the contraction itself came to be known as "synapsis." But it has been shown that conjugation may either precede or follow the contraction, and that it occurs in nuclei showing no contraction whatsoever. Moreover, the contraction is in some measure an artifact. It is therefore now customary to refer to chromosome conjugation as *synapsis*, and to the contraction, natural or otherwise, as *synizesis*.

In an increasing number of reported cases the paired association begins during the anaphase and telophase of the last premeiotic mitosis. As a recent example may be cited the case of the fly, *Asilus sericeus* (Metz and Nonidez, 1921), in which the pairing, already evident in the premeiotic anaphase, becomes an intimate synaptic union in the telophase. In the following prophase these bivalent chromosomes develop directly into diplotène threads; the ordinary leptotène stage is lacking.[1] Furthermore, the pairing begins in the spermatogonia several cell generations before meiosis in a number of instances.[2] Again, cases are now known in which the synaptic attraction is shown in some measure in the somatic cells; in extreme examples the pairing occurs directly after the gametic chromosome sets are brought together in syngamy, and persists throughout development. This is notably true of the Diptera. The chromosomes in the somatic cells of these flies show a conspicuously paired arrangement in the metaphase (Figs. 182, 203). Metz (1916*a* etc.) has found this in a great many species, and in some cases the union, which begins during the early cleavage divisions of the fertilized egg, is at certain stages so close that it practically amounts to a synapsis. In some cases it seems that such an appearance may be due to inadequate fixation (Whiting, 1917, on *Culex*). A loosely paired arrangement is also frequently reported in the somatic cells of plants,[1] but apparently no real synapsis occurs until the meiotic phase is reached.

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[1] Some degree of synaptic union in the premeiotic telophase was observed earlier by Montgomery (1900, 1901) in certain Hemiptera; Nichols (1902) in *Oniscus;* Sutton (1902) in *Brachystola;* Blackman (1903, 1905) in *Scolopendra;* and Dublin (1905) in *Pedicellina.*

[2] Certain Hemiptera and *Ascaris* (Montgomery, 1904, 1905, 1908, 1910); *Alytes* (Janssens and Willems, 1909); *Helix* and *Sagitta* (Stevens, 1903; Ancel, 1903); certain Diptera (Stevens, 1908, 1911); *Pediculus* (Doncaster, 1920).

**The Relationship of the Synaptic Mates.**—It remains to inquire further into the relationship of the two chromosomes which unite to form a synaptic pair. Is any chromosome of the diploid complement free to pair with any other, or does the pairing proceed according to more definite rules? It was suggested by Henking (1891) that the synaptic mates are descendants of chromosomes contributed by the two parents through the gametes at the previous syngamic union: the chromosomes of one gametic set pair with those of the other gametic set to form the haploid number of bivalent chromosomes. A significant additional suggestion was made by McClung (1900), Montgomery (1901), and Sutton (1902): not only are the two synaptic mates derived from the two gametes, but they are homologous—each chromosome of one gametic set pairs

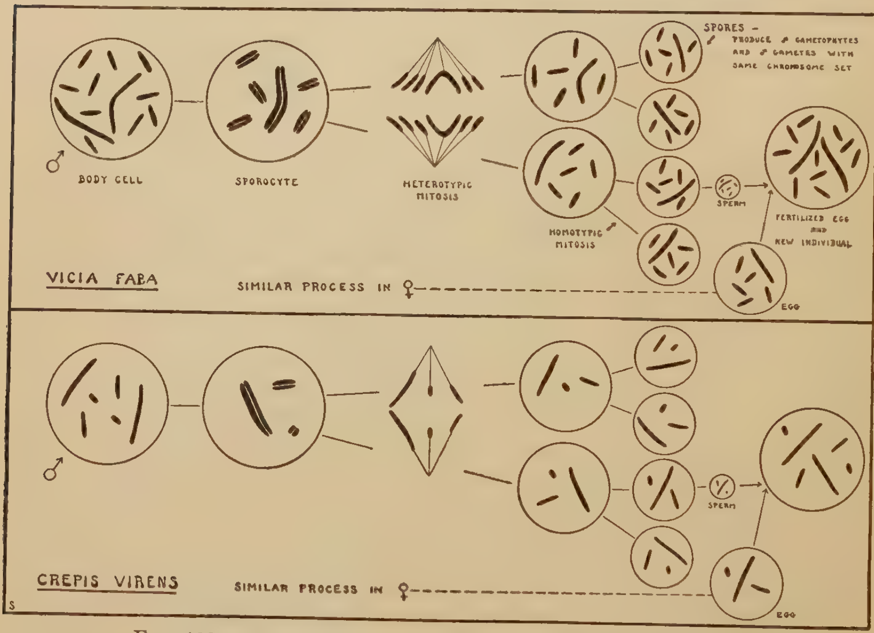

FIG. 123.—Chromosome cycles in *Vicia faba* and *Crepis virens*.

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[1] Strasburger (1905, 1907, 1910*a*) on *Galtonia candicans, Funkia Sieboldiana, Pisum sativum, Melandrium, Mercurialis,* and *Cannabis;* Sykes (1908) on *Hydrocharis, Lychnis, Begonia, Funkia, and Pisum;* Overton (1909) on *Calycanthus;* Müller (1909, 1911) on *Yucca* and other forms; Stomps (1910) on *Spinacia;* Kuwada (1910) on *Oryza;* Tahara (1910) on *Morus;* Ishikawa (1911) on *Dahlia.*

with a particular member of the other gametic set, the two members of each pair having the same general rôle in the life of the organism and being of corresponding hereditary value. Substantial support for this important hypothesis was found in organisms with chromosomes differing characteristically in size and shape. A large number of such cases have now been described, so that homologous pairing is no longer a hypothesis but a demonstrated fact.

Simple illustrations of homologous pairing are given in Fig. 123. In *Crepis virens* there are six chromosomes: two long, two of medium size, and two short. When synapsis occurs the like chromosomes pair, forming bivalents of three sizes. The members of each pair disjoin in the meiotic divisions, each microspore having as a result three chromosomes: one long, one medium, and one short. Since the gamete contains such a haploid set of three chromosomes, and the somatic cells of the new individual show six (two of each length), it is evident that the other gamete furnishes a similar haploid set of three (Rosenberg, 1909).

[illegible]

In *Vicia faba* there are in the somatic cells twelve chromosomes, two of them being twice as long as the other ten (Figs. 63, 123). At synapsis in the microsporocyte there are formed six bivalents, one of these having about twice the length of the other five; hence it is plain that the two long chromosomes pair with each other. In the ensuing mitoses the synaptic mates disjoin. At the close of the second mitosis the microspore, and therefore the male gamete to which it later gives rise, contains a haploid set of six chromosomes: one long and five short. Since the somatic nuclei contain each of these in duplicate, it is evident that a similar set is contributed by the female gamete (Sharp, 1914; Sakamura, 1915, 1920).

Vicia

The foregoing typical cases show clearly that in normal life cycles the diploid chromosome complement is composed of two intermingled haploid sets of unlike chromosomes, these two sets being brought together by the fusion of the gametes. The two members of each synaptic pair are derived from the two gametic sets, of which they are homologous members. That homology, and not simple parental derivation, is the important characteristic of the synaptic mates is evident in the phenomena observed in polyploid and hybrid organisms.

Among both plants and animals there are known many cases of *polyploidy*, the somatic cells showing not merely two intermingled haploid sets (diploidy), but three (triploidy), four (tetraploidy), or more. In some cases such conditions are known to be due to hybridization, and can be produced at will, as by crossing a tetraploid with a diploid to produce a triploid. In other cases, however, the origin of the polyploid condition is less clear. Chromosome behavior in polyploid organisms throws interesting light on synapsis, since such forms contain three or more homologues in their nuclei, rather than the normal two.

In the first place, synapsis in some polyploid organisms results in the union of all the homologues present. This is notably the case in *Datura:* in triploid and tetraploid plants which have respectively three and four chromosomes of a kind (trisomes and tetrasomes) instead of simple pairs (disomes), trivalent and quadrivalent groups appear in the sporocytes (Belling and Blakeslee, 1922, 1923, etc.; Belling, 1923). Hence it is clear, particularly in the case of triploids known to be due to the union of haploid and diploid gametes, that two homologous chromosomes may pair even if they are contributed by the same gamete. The same behavior is seen in triploid types of *Canna* (Belling, 1921), *Morus* (Osawa, 1920), and *Zea* (Randolph, 1926). In some types of *Zea*, however, the extra chromosomes form trivalents or quadrivalents in some sporocytes but remain separate in others, which indicates the need of caution in attributing lack of synapsis to an absence of homology. On the basis of observed genetic ratios it has been concluded that the members of the trisome in *Datura* are distributed at random in meiosis. The same appears to be true of the members of the tetrasome in tetraploid *Daturæ;* but in *Triticum* (Sax, 1922) they seem to show regular selective pairing and disjunction, as in diploid plants. Blakeslee speaks of this latter type of plant as a "double diploid" rather than a "true tetraploid." In flies, which so often show conspicuous somatic chromosome pairing, groups of three and four occur in the somatic cells of triploid and tetraploid individuals (Metz, 1916, 1922*c*; Holt, 1917; Bridges, 1922). In case each homologue shows its split in the prophase or metaphase of the first meiotic mitosis, a trivalent chromosome appears as a *hexad* (six chromatids) and a quadrivalent as an *octad* (eight chromatids).

In contrast to the condition in *Datura,* synapsis in certain other polyploid hybrids leads to the formation of bivalents only, no larger groups appearing. Our definite knowledge in this field began with the observations of Rosenberg (1909) on *Drosera* hybrids. When *Drosera rotundifolia* (20 chromosomes) is crossed with *D. longifolia* (40 chromosomes) there results a hybrid with 30 chromosomes, of which 10 are contributed by *rotundifolia* and 20 by *longifolia.* When synapsis occurs in the microsporocytes in this hybrid only 10 bivalents are formed, 10 chromosomes remaining unpaired. This was taken by Rosenberg to mean that the 10 *rotundifolia* chromosomes pair with 10 of the *longifolia* ones, leaving the other 10 of *longifolia* without synaptic mates. Had any chromosome of the entire group of 30 been free to pair with any other, 15 bivalents would have been produced. Strasburger, however, was of the opinion that the homology of the 20 chromosomes in the diploid gametic *longifolia* complement had led to their pairing, leaving the 10 *rotundifolia* chromosomes without mates. Subsequently described cases have thrown an interesting light upon this matter.

In certain cases the numerical relations of the chromosomes are such as to show that all of the members of the smaller gametic complement pair with an equal number of members of the larger gametic complement, leaving the remainder of the latter complement unpaired, as Rosenberg concluded for *Drosera*. Thus in *Rosa* hybrids with 28 (tetraploid), 35 (pentaploid), and 42 chromosomes (hexaploid) there are always seven pairs present at meiosis, the extra chromosomes (14, 21, and 28 in the three types) remaining unpaired (Fig. 183) (Täckholm, 1920, 1922). Likewise in *Triticum* hybrids with 35 chromosomes (14 Emmer + 21 Vulgare) there are formed 14 synaptic pairs, leaving seven unpaired univalents (Kihara, 1919; Sax, 1922). This "*Drosera* type," or "$F_1$ type," of chromosome behavior in hybrids, of which many instances are known, will be described more fully in Chapter XVII.

Further studies have shown that in some cases a pairing of the extra chromosomes brought in by the gamete with the larger number may also occur. In certain *Hieracium* hybrids Rosenberg (1917) observed more gemini than would be expected from the number of chromosomes in the smaller parental complement, and concluded that some of the extra chromosomes were themselves homologous and had paired. This conclusion receives striking confirmation in *Digitalis*, *Solanum*, *Papaver*, and *Crepis*.

In certain *Digitalis* hybrids with 72 chromosomes (48 *lutea* + 24 *micrantha*) 36 gemini appear at diakinesis (Haase-Bessell, 1921). Similarly, Winkler (1916) reported that in *Solanum nigrum* hybrids with 108 chromosomes (36 + 72) there are 54 gemini formed. In *Papaver* hybrids with 42 chromosomes (7 *nudicaule* + 35 *striatocarpum* or *radicatum*) there are 21 gemini at diakinesis, showing that there has been a synapsis not only of chromosomes from the two gametic complements ("allosyndesis"), but also of chromosomes from the same gametic complement ("autosyndesis") (Ljungdahl, 1924). In *Crepis* hybrids with 24 chromosomes (4 *setosa* + 20 *biennis*) the microsporocytes show 10 gemini and 4 unpaired chromosomes, which is taken to mean that the *biennis* chromosomes have conjugated among themselves, leaving the 4 *setosa* chromosomes unpaired (Collins and Mann, 1923). The failure of the latter to undergo synapsis *inter se* probably indicates that they represent a basic haploid set including no homologues.

A particularly close relationship of synaptic mates is seen in diploid *Datura* plants obtained by selfing haploids. If the haploid plant has arisen, as seems probable, by the parthenogenetic development of an egg with 12 chromosomes, any two homologous chromosomes brought together by the union of two of its 12-chromosome gametes and later undergoing synapsis are descendants of the same chromosome. The chromosomes in the microsporocytes of the haploid plant show no synaptic attraction whatsoever; there are no homologues. Another case in point is that of *Rhabditis monohystera*, a parthenogenetic nematode worm. The 20 chromosomes in the oöcyte form 10 synaptic pairs and separate in the single meiotic mitosis which occurs. During the telophase of mitosis the chromosomes appear divided, as in ordinary meiosis, but since there is no second mitosis to separate them the egg retains the diploid number, 20. This egg develops without syngamy into a diploid animal, and at the next meiosis the 20 chromosomes form 10 gemini as usual. Hence any two synaptic mates have descended from the same original chromosome (Bělař, 1923).

All of these cases make it plain that the essential characteristic of synaptic mates is their homology, and not merely their parental derivation. In normal cross-fertilized organisms the two synaptic mates are contributed by the two parents; in self-fertilized organisms they are derived from the same parent but through different gametes; in certain hybrids and other cases they may be derived from the same gamete. The pairing of the extra chromosomes in hybrids probably indicates a homology of some of them, as Rosenberg suggested. In such cases at least one of the gametic complements itself comprises more than a simplex haploid set of chromosomes, its members consequently exhibiting their ability to pair. In other hybrids there is a much reduced tendency to form pairs, synapsis in some cases being wholly lacking (Chapter XVII). Very little is known about the factors which bring about the synaptic union, but there is much evidence that the mutually attractive homologues show similar structural characteristics, and the genetic data indicate a corresponding of hereditary function also. Furthermore, it may be expected that a closer examination of the early stages of the meiotic prophase in polyploid and hybrid organisms will lead to information of considerable value in interpreting these stages in normal diploid forms.

It may further be pointed out that, although the essential feature of meiosis in all cases is a reduction in the number of homologous chromosomal elements present in the nucleus, the numerical change in polyploid organisms may actually be from four to two, or from six to three, and so on, rather than from two to one as in ordinary diploid forms.

**The Nature of the Synaptic Union.**—The crux of the whole problem of synapsis lies in the question of what takes place between the conjugating members: do they actually fuse, wholly or partially, or do they simply undergo a temporary pairing, with or without "interchange of influence?" No point in cytology is of greater interest to the geneticist than this one.

A survey of the several interpretations of meiosis outlined in previous pages shows that they involve synaptic associations of various durations. In cases with no formation of bivalents before diakinesis or the metaphase of *I* (granting that such a condition may exist) the association is only momentary, and there appears to be very slight opportunity for mutual influence, particularly in the case of telosynaptic tetrads.

According to *Scheme B*, the synaptic mates, whether or not they are in contact end-to-end in the early prophase of *I*, do not assume a side-by-side arrangement until later in the prophase, after they are partially shortened and thickened. According to *Scheme A*, the conjugation begins with the lateral association of the leptotène threads very early in the prophase (or even with a premeiotic association in exceptional cases), and continues throughout the prophase and metaphase of *I* (or through the metaphase of *II* in the case of postreduction). Concerning the closeness of the parasynaptic association, however, opinions have differed rather widely, since the constitution of the pachytène threads is very difficult to make out.

A few investigators[1] have thought that the conjugating members fuse so completely that their identity is lost, the resulting "mixochromosome" then undergoing two longitudinal splits along entirely new planes in the two meiotic divisions. Many investigators have supposed that the identity of the two fusing members is not thus lost, the first "resplitting" being along the synaptic plane. Perhaps the most widely held view has been that the synaptic threads undergo no actual fusion, but maintain their identity completely. Often their association is so intimate that they seem to form a simple thick thread, but the doubleness reappears during the later stages.[2] Several careful observers have reported that the doubleness is visible at all stages in properly fixed preparations.[3]

The behavior of chromomeres in parasynapsis has been variously interpreted. Strasburger (1904, 1905) conceived synapsis to be primarily a conjugation of smaller chromatic units within the chromosomes, such a conjugation or fusion involving an interchange of still smaller units, such as the "pangens" of de Vries. Likewise C. E. Allen (1905) and a number of more recent writers (Agar, 1923) have maintained that the fusion of the leptotène threads involves a fusion of the chromomeres, whose subsequent division initiates the resplitting of the pachytène thread. The evidence for the behavior of chromomeres as autonomous units in synapsis has frequently been criticized as inadequate.[4] Subsequent researches have shown that, although this criticism has been justified in many cases, there are instances in which the chromomeres actually represent structural differentiations in the chromosomes. Notable in this connection are the often cited observations of Wenrich (1916, 1917) on *Phrynotettix magnus*, a grasshopper. Here the chromomeres in the two homologous chromosome threads show the same characteristic sizes and arrangement, and in the synaptic process corresponding chromomeres are brought opposite each other (Fig. 65). Such a correspondence in the chromomeres of pairing homologues has also been shown in the flatworm, *Dendrocœlum lacteum*, by Gelei (1921, 1922) and in a marsupial, *Macropus ualabatus*, by Agar (1923). Contrary to Wenrich, these observers claim that the pairing threads actually fuse. According to Agar this involves a fusion of their chromomeres, but Gelei states that these remain distinct, so that the pachytène thread is always constitutionally double. Technical difficulties have so far largely prevented an exact determination of the behavior of chromomeres in either the somatic or meiotic phases, but it seems clear that, although their appearance may be far from natural in fixed preparations, they "correspond to real local differentiations of the substance of the chromosome" (Agar). The general opinion is that such differentiations bear some relation to the units of inheritance which seem to be in some way regrouped during the process of synapsis.

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[1] Vejdowský (1907), Bonnevie (1906, 1908, 1911), von Winiwarter and Sainmont (1909), H. Schneider (1914).

[2] Berghs (1904, 1905), A. and K. E. Schreiner (1905, 1906), Maréchal (1907), J. B. Overton (1905, 1909), Robertson (1915, 1916).

[3] Grégoire (1907, 1910), Schleip (1906, 1907), Montgomery (1911), Kornhauser (1914, 1915), Wenrich (1915, 1917).

[4] See the discussions by Grégoire (1907, 1910).

*Chiasmatypy.*—One of the most important suggestions made concerning synapsis is embodied in the Theory of Chiasmatypy, originally advanced by Janssens (1909) as a result of his studies on the salamander *Batracoseps attenuatus*, and more recently supported by his outstanding work on the insects *Stethophyma grossum* (*Mecosthethus grossus*) and *Chorthippus* (*Stenobothrus*) *curtipennis* (1924). According to this theory, the two synaptic mates undergo an intimate fusion (chiasma) at one or more points through which separation later occurs along a new plane, so that each of the two chromosomes which finally pass apart in the anaphase is made up of one or more portions of each of the original synaptic mates. If such a process occurs before the conjugating threads split (Fig. 124), all four gones will have the altered chromosomes ("complete chiasmatypy"); but if it occurs after the splitting, the exchange may involve only two of the four chromatids, so that only two of the four gones will have the altered chromosomes ("incomplete chiasmatypy," the more common type; Fig. 125, *C*). Decisive evidence for chiasmatypy has been exceedingly difficult to obtain, and that originally submitted by Janssens has been considered unconvincing by several

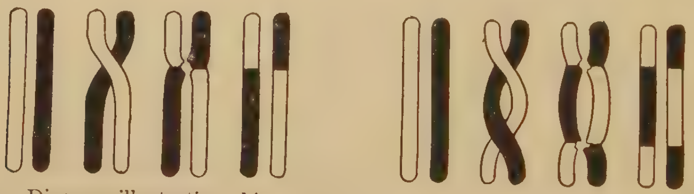

FIG. 124.—Diagram illustrating chiasmatypy in unsplit homologous chromosomes. One chiasma at left; two chiasmas at right. (*Adapted from Babcock and Clausen.*)

cytologists,[1] who pointed out that such appearances could be interpreted without recourse to the theory of chiasmatypy, particularly in the case of the multiple ring tetrads of certain orthopterans (Fig. 126, *V*, *X*).

In his later researches Janssens (1924) found a particularly favorable object in *Stethophyma grossum.* The chromosomes in this insect are marked by a "proximal granule" at the end to which the spindle fibers attach; they form no loops, and pass through no confusing pachynema stage. The leptotène threads, oriented with their proximal ends toward one side of the nucleus, form 11 bivalent pairs. In each pair the two threads unite closely at only one point; elsewhere they remain apart, and show no splitting until the diplonema stage. Several modes of synapsis may occur, according to the location of the single principal point of union (Figs. 125, 126). When the union is at the proximal end the resulting tetrad is inserted on the spindle in *I* by its middle point (the synaptic point, as indicated by the proximal granules); here *I* is equational and *II* disjunctional (Fig. 125, *A*). When the union is at the distal end *I* is disjunctional and *II* equational (Fig. 125, *B*). If the union occurs at some intermediate point (apparently it may occur almost anywhere), the tetrad takes the form of a cross in which each synaptic mate (two chromatids) makes up one of the vertical and one of the horizontal arms (Fig. 125, *C*). In such cross tetrads chiasmatypy occurs. Usually only one chromatid of each mate breaks and unites with one of the other mate at the crossing point; here *I* is equational for the horizontal arms and disjunctional for the vertical arms, and *II* is accordingly disjunctional and equational for these portions respectively. More complex conditions may result from the presence of more than one chiasma. Since the various types of tetrads may occur in the same cell, each meiotic division may be disjunctional for some chromosomes, equational for others, and partly disjunctional and partly equational for still others. That an interchange of parts of chromosomes actually occurs is held by Janssens to be proved by the sharp angle made by one chromatid as opposed to the straight course of its companion at the point of crossing, the clear breaks seen in two of the chromatids as compared with the unbroken nature of their respective companions, and the visible composite nature of two of the four chromatids as they move apart in the anaphase of *I* (Fig. 126, *I*, *J*, *S*, *U*, *W*).

Little direct evidence for chiasmatypy other than that contributed by Janssens has as yet been reported. Gelei (1921) figures twisted prophase chromosomes of *Dendrocœlum* which he thinks may bring about a regrouping of the chromomeres when the pachytène thread resplits (Fig. 118, *H-J*). Robertson (1921) reports that in the tetrads of *Chorthippus* the two chromatids of one synaptic mate show one complete revolution about

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[1] Wilson (1912*b*, 1920), Robertson (1916), Wenrich (1916, 1917), McClung (1924). More recently Robertson (1921) favors the theory.

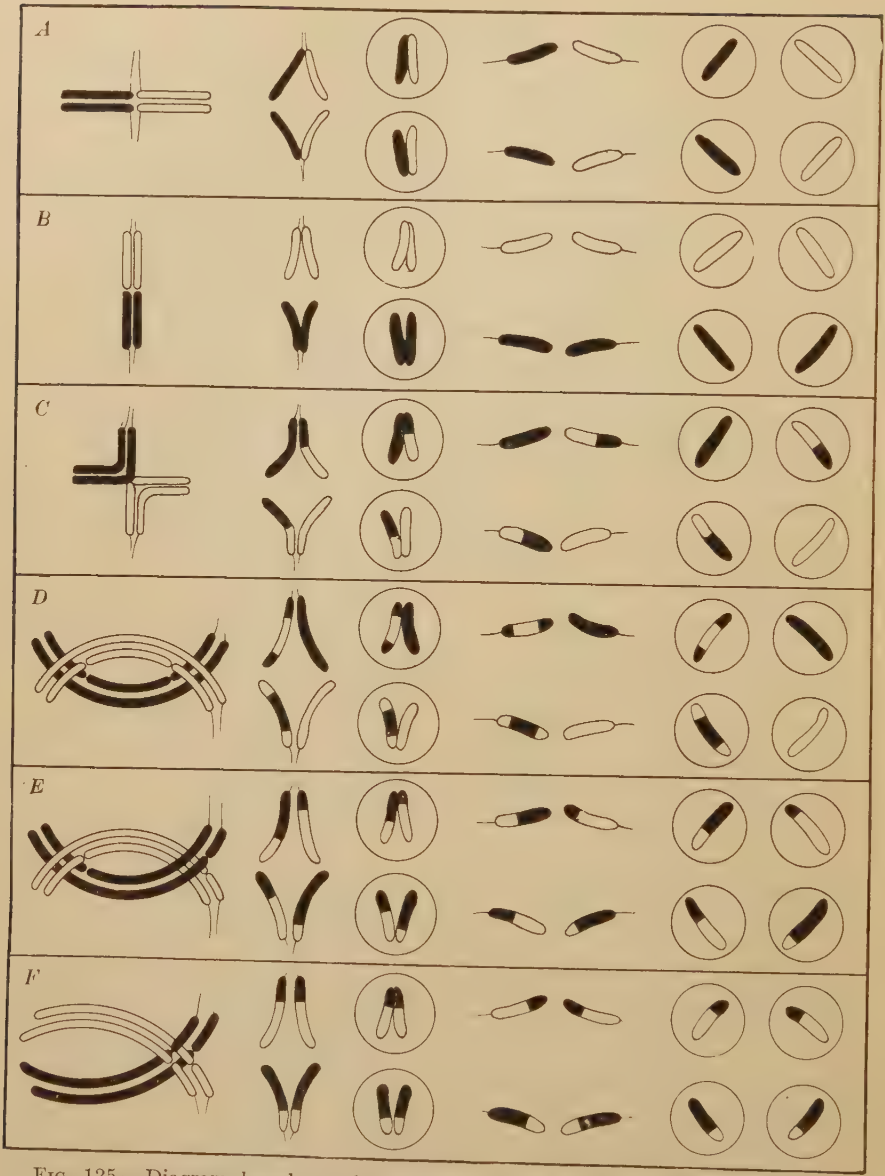

FIG. 125.—Diagram based on the schemas of Janssens (1924) illustrating various modes of behavior of the tetrad chromosomes in orthopterans. *A*, proximal telosyndesis; no chiasmatypy. *B*, distal telosyndesis; no chiasmatypy. *C*, incomplete chiasmatypy in cross tetrad; with respect to the elements of this tetrad the quartet nuclei are of 4 kinds, two of them having altered chromosomes. *D*, incomplete double chiasmatypy (involving only 2 of the 4 chromatids); quartet nuclei of 4 kinds, 2 having altered chromosomes. *E*, complete double chiasmatypy (involving all 4 chromatids), but with the two chiasmas at different loci; quartet nuclei of 4 kinds, all with altered chromosomes. *F*, single chiasmatypy involving all 4 chromatids, but at the same locus; nuclei of quartet are of 2 kinds and all have altered chromosomes, as after chiasmatypy of unsplit chromosomes (Fig. 124). (The chromatids are supposed to exchange segments at the points where they are shown broken.)

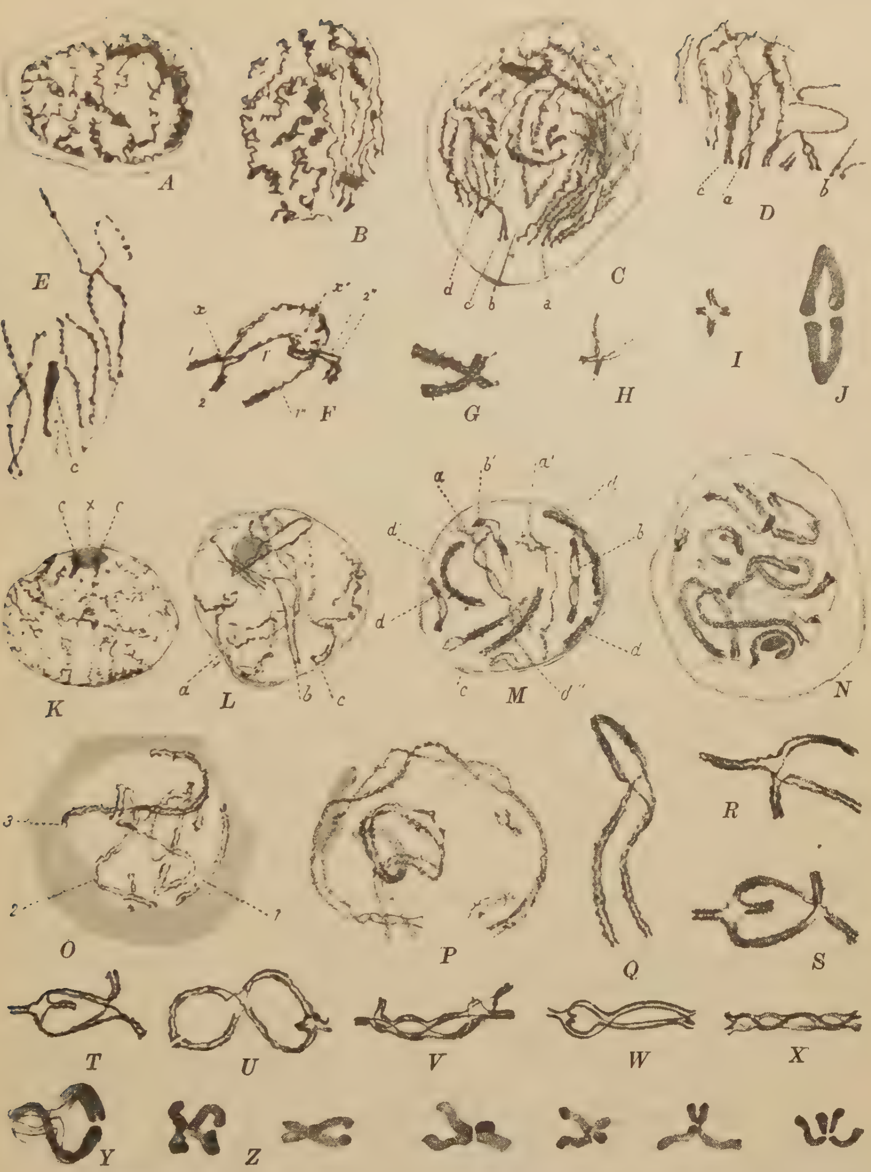

Fig. 126.—Meiosis in the spermatocytes of *Stethophyma grossum* (*A–J*) and *Chorthippus parallelus* (*K–Z*). *A*, preleptotène nucleus. *B*, leptotène. *C*, parallel leptotène threads. *D*, *E*, pairing threads with chiasmas. *F*, diplotène; each member split. *G*, *H*, later stages. *I*, cross tetrad with breaks at two of the angles. *J*, anaphase, showing breaks presumably due to exchange of segments. *K*, preleptotène threads in *Chorthippus*. *L*, threads becoming parallel. *M*, amphitène nucleus. *N*, pachytène. *O*, pachytène; synapsis in one pair incomplete because of entangled thread. *P*, diplotène. *Q*, *R*, diplotène, with members split. *S*, *T*, tetrads with thin spots at angles. *U–X*, more complex figures due to presence of more than two contacts or chiasmas. *Y*, early anaphase of division *I*, showing relation of chromatids. *C*, six figures showing breaks in chromosomes at the metaphase of division *II* ("late chiasmatypy"). (*After Janssens*, 1924.)

each other, the other mate not being so twisted; this may be the result of chiasmatypy.

In addition to the process described above, Janssens reports certain evidence indicating that an exchange of chromosome segments ("late chiasmatypy") occurs during the metaphase of *II* and possibly also of *I* (Fig. 126, *Z*); and furthermore that appearances in somatic cells suggest chiasmatypy there as well. Hence it may be that chiasmatypy is a general chromosomal process which has a special significance for heredity only in the meiotic phase when the elements concerned are qualitatively different. Chodat (1925) also believes that an interchange of portions of chromosomes may take place in the metaphase of *I*. In *Allium ursinum*, according to his interpretation, the crossed free ends of the synaptic mates come to lie side-by-side in the equatorial plane, each of these ends then undergoing a division in this plane. The halves of each end-portion are then carried to opposite poles by the disjoining homologues, *I* being equational for the end-portions alone. These suggestions call for further careful examination of the first meiotic metaphase and anaphase.

*Rhegmatypy.*—Another suggestion regarding the interchange of segments of chromosomes has been put forward by Prell (1921, 1923*a*) in his Theory of Rhegmatypy. This theory is based largely on fluctuations in chromosome number through temporary fragmentation observed by other workers, principally by Seiler (1919, 1922) in butterflies. In *Solenobia pineti* Seiler found three races, showing 30, 31, and 32 chromosome pairs respectively, the population consisting of these races and their various hybrids. The diploid number may therefore range from 60 to 64, but only cases with 61, 62, and 63 were observed. In the hybrids there are always 30, 31, or 32 bivalents, with no unpaired univalents; hence one parental complement must assume the form of the other parental complement, at least through the synaptic period. Seiler's hypothesis is that one of the chromosomes in the species is a triple complex, which appears single in the 30-chromosome race, but which subdivides into two and three parts in the 31-chromosome and 32-chromosome races respectively; and, further, that in synapsis in a hybrid one chromosome of the pair temporarily assumes the combined or the divided form of the other. Later, in the gamete or embryo, the altered chromosome resumes its original form.

As a result of this and other observations on fluctuations in number within individuals and clones (*Narcissus*, *Najas*, *Ascaris*), and the apparent results of fragmentation within larger systematic groups (Drosophilinæ; Metz), Prell advances the theory that the chromosomes may undergo a fragmentation as the result of certain environmental conditions, and a subsequent reunion ("syzygie") at meiosis, and that irregularities in the reunion may bring about a regrouping of the parts.

In this way an actual interchange of parts between homologues takes place.

It will be observed that the process of rhegmatypy is not very different from the "late chiasmatypy" of Janssens, whereby segments of chromosomes are supposed to be interchanged in the metaphase of one or the other of the meiotic mitoses in addition to earlier more typical chiasmatypy. All of these phenomena may be looked upon as the result of a tendency on the part of chromosomes, which seem to be compound bodies, to undergo a partial and temporary separation into component elements under certain conditions prevailing at different stages of the chromosome cycle. If it is true that corresponding segments of two homologous chromosomes exchange places through chiasmatypy or rhegmatypy, the chromosome which can be followed as an individual through successive generations must be thought of not as an unvarying unit, but rather as a persistent system whose constituent parts may occasionally be replaced by homologous elements. The great significance of such phenomena for genetics will be discussed in Chapter XX.

**Conclusion.**—In concluding this consideration of meiosis we may revert to the summary on page 256, which is a statement of the fundamental facts underlying the discussions of heredity that are to follow in later chapters.

# CHAPTER XIV

## GAMETOGENESIS

The gametes or sexually fusing elements of various organisms differ so widely in their structure and mode of origin that any complete description of all types in a single chapter is obviously impossible. We shall therefore take up a series of more or less typical cases, dealing in detail only with certain features of particular interest. Accounts of the general morphology of gametogenesis may be found in a number of textbooks and more special works on botany and zoölogy.

**Algæ and Fungi.**—It is among the algæ and fungi especially that great diversities in features associated with gametogenesis are encountered. As is well known, the two gametes involved in a sexual fusion may be morphologically similar or dissimilar, and motile or non-motile. They are similar and motile in *Ulothrix* and *Ectocarpus*, the two cilia being equal and terminally inserted in the former, and unequal and laterally inserted in the latter. In *Spirogyra* the gametes are but slightly modified vegetative cells with no special motile apparatus. In *Mucor* they are multinucleate masses of protoplasm (*cœnogametes*) separated from the rest of the body by walls. In some such forms the two gametes may give in their behavior a clear indication of physiological differentiation, and sometimes they differ in size as well.

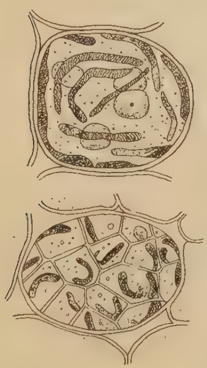

Fig. 127.—Two stages in the development of gametes in a brown alga, *Stictyosiphon.* Several divisions of the nuclei and plastids occur, after which the protoplasm is subdivided into gametes with one nucleus and one plastid each. (*After Kuckuck.*)

Well-known instances of the complete differentiation of the gametes into large non-motile eggs and small motile spermatozoids are seen in *Œdogonium*, *Fucus*, and *Vaucheria*. In *Œdogonium* certain small cells of the filament produce two oval spermatozoids, each with a ring of cilia around one end, while the contents of other cells of normal size enlarge and become eggs (Fig. 153, *C*). The egg is well supplied with plastids and reserve food materials, and a more or less clear "receptive spot" may often be made out at the point where the spermatozoid is to enter. In *Fucus* the primary nucleus of the antheridium initiates a series of mitoses giving rise to a large number of nuclei. About each of these is organized a spermatozoid. In the oögonium the primary nucleus initiates a series of three mitoses, the protoplasm then subdividing to form eight eggs. In *Ascophyllum* only four eggs are formed, the other four nuclei degenerating. In *Pelvetia* there are two eggs, and six degenerating nuclei. In *Cystosira* and *Sargassum* seven of the eight nuclei degenerate, most of the contents of the oögonium organizing as a single egg. In *Vaucheria*, which is cœnocytic, many spermatozoids are organized about the nuclei in the antheridium, but in the oögonium all of the nuclei but one, together with many of the plastids and much cytoplasm, pass back into the supporting filament before the oögonium is separated off by a wall; hence the egg is uninucleate, and like many other eggs it shows a well-differentiated receptive papilla (Fig. 128).[1]

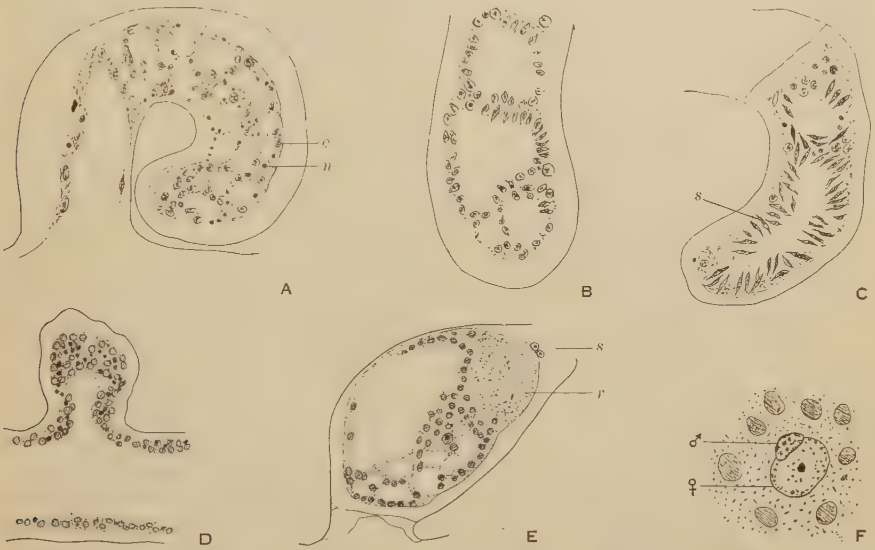

Fig. 128.—Gametogenesis and syngamy in *Vaucheria sessilis*. *A–C*, differentiation of spermatozoids in cœnocytic antheridium. *D*, early stage in development of oögonium. *E*, mature egg, with one nucleus and many plastids. *F*, male and female nuclei uniting in egg. *c*, chloroplast; *n*, nucleus; *r*, receptive papilla; *s*, spermatozoids. (*After Oltmanns*, 1895.)

Finally, in the red algæ and the oömycetes are forms with unlike gametes, both of which are non-motile. In *Polysiphonia* non-motile male gametes, or "spermatia," are budded off successively from the antheridial cell; each of them is supplied with a nucleus formed by the mitotic division of the antheridial nucleus. The female nucleus here lies in the base of the carpogonium, a cell which elongates to form a receptive

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[1] Pringsheim (1858), Thuret (1854–1855), Klebahn (1892), Oltmanns (1889, 1895), Nienburg (1910), Sauvageau (1909-1911), Farmer and Williams (1898), Kylin (1916, 1920), Yamanouchi (1909), and others. For a full account of the algæ, see Oltmanns (1922–1923).

"trichogyne" above. In the oömycetes,[1] which are cœnocytic, the female gamete may be multinucleate (*Albugo bliti*), but seems more often to be uninucleate (*Albugo candida, Saprolegnia*). In *Albugo bliti* many of the nuclei originally present in the young oögonium remain functional, but in *A. candida* and *Pythium Debaryanum* all but one retreat to the periplasm, which becomes rather sharply set off from the central oöplasm with the single functional nucleus (Fig. 129). The egg in these forms contains another cytoplasmic body, the *cœnocentrum*, whose origin and function are not understood. In *Saprolegnia* the multinucleate protoplasm of the oögonium becomes divided up by one or more vacuoles into several eggs, in each of which all but one of the nuclei degenerate (Fig. 130). The male gametes of the oömycetes are represented by the multinucleate protoplasm of the antheridia; in some cases (*Albugo bliti*) a number of male nuclei may later enter the egg (p. 324), but in others (*Albugo candida*) only one enters, as a rule. The only motile gametes in fungi are the spermatozoids of *Monoblepharis*, which have a single cilium. Sexual phenomena in ascomycetes and basidiomycetes are discussed in the next chapter.

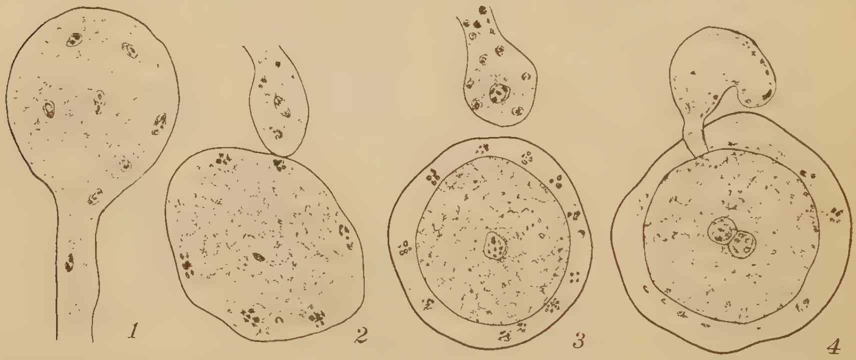

FIG. 129.—Gametogenesis and syngamy in *Pythium Debaryanum*. 1, formation of oögonium at end of hypha. 2, oögonium and antheridium in contact. 3, egg mature; degenerating nuclei in periplasm; antheridium above, with one functional and several non-functional nuclei. 4, sexual nuclei in contact. (*After Miyake*, 1901.)

The details of the process of spermatogenesis in the algæ have frequently been examined, but zoöspores have been preferred for such investigations because of their usually larger size. Male gametes and zoöspores in each of several groups of algæ show the same characteristic type of structure, and there is much to suggest that the former have been phylogenetically derived from the latter. The protoplasm of the antheridium or the sporangium, as the case may be, may or may not be entirely used up in the formation of the spermatozoids or the zoöspores. At the beginning of the process the chromatophore, if it is large and continuous as in *Cladophora*, takes the form of numerous smaller plastids, and the pyrenoids and starch gradually disappear. In large sporangia a central vacuole may develop. What is evidently vacuolar material then appears in clefts or as rounded coalescing masses, and divides the protoplasm into a number of polygonal or rounded uninucleate units, which for some time may not become wholly free from one another. In each of these there differentiates one eyespot, and also a motor apparatus, consisting chiefly of a blepharoplast with its attached cilia.

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[1] Trow (1895–1904), Wager (1896, 1900*b*), Stevens (1899, 1901), B. M. Davis (1900, 1903, 1905), Miyake (1901), Claussen (1908).

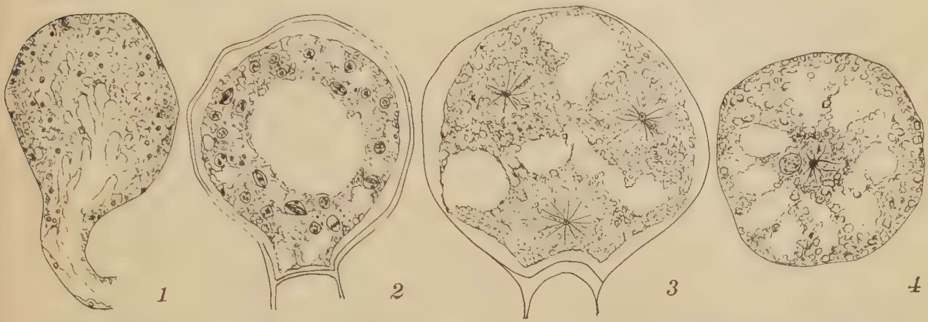

FIG. 130.—Oögenesis in *Saprolegnia*. 1, oögonium forming at end of hypha. 2, nuclei multiplying. 3, subdivision of protoplasm to form several large eggs, each with a cœnocentrum. 4, single egg, with nucleus and cœnocentrum. (*After B. M. Davis*, 1903.)

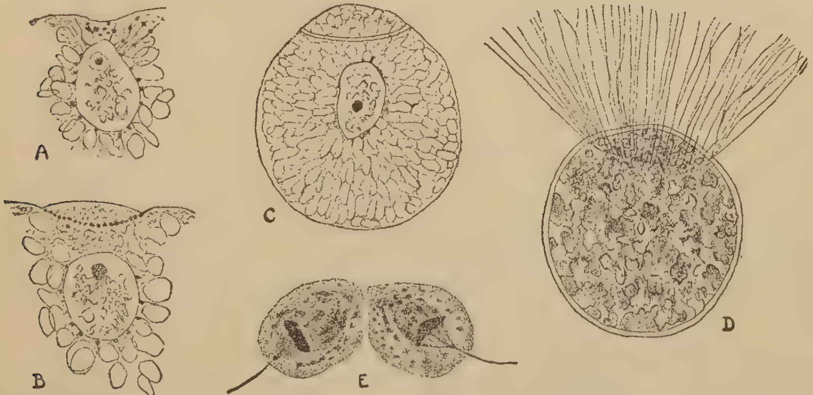

FIG. 131.—*A–D*, formation of the cilia-bearing ring in the zoöspore of *Derbesia*. (*After Davis*, 1908.) *E*, *Stemonitis flaccida;* cilia growing from centrosomes during late stage of division in the formation of swarmers. (*After Jahn*, 1904.)

The development of the *blepharoplast*, or cilia-bearing organ, has attracted much interest in these and other organisms. In the immature zoöspore of *Œdogonium* Strasburger (1892, 1900*a*) found that the plasma membrane, apparently under the influence of the nucleus, develops a lens-shaped thickening from which the cilia grow out; at the base of each cilium is a minute refractive granule. Each of the many pairs of cilia on the *Vaucheria* swarm spore is associated with a nucleus lying near the cell membrane. In *Hydrodictyon* (Timberlake, 1902) and *Rhodochytrium* (Griggs, 1904) the cilia grow out from a small body which lies near the plasma membrane and is connected with the nucleus by delicate protoplasmic strands. In *Derbesia* (Davis, 1908) the nucleus migrates toward the plasma membrane, and from it many granules move out along radiating cytoplasmic strands to the surface of the cell, where by fusion they form a ring-shaped structure from which the cilia grow out (Fig. 131). In the spermatozoid of *Chara* the blepharoplast, which bears two cilia, appears to arise as a differentiation of the plasma membrane (Belajeff, 1894*a*; Mottier, 1904*a*). Such blepharoplasts as those of *Chara* and *Œdogonium* are known as "plasmodermal blepharoplasts." In *Eudorina*, according to Hartmann (1921), the pointed end of the nucleus, to which a centriole is attached, touches the membrane and then retreats to the center of the cell, leaving behind a double body (centrioles?) from which the cilia grow out.

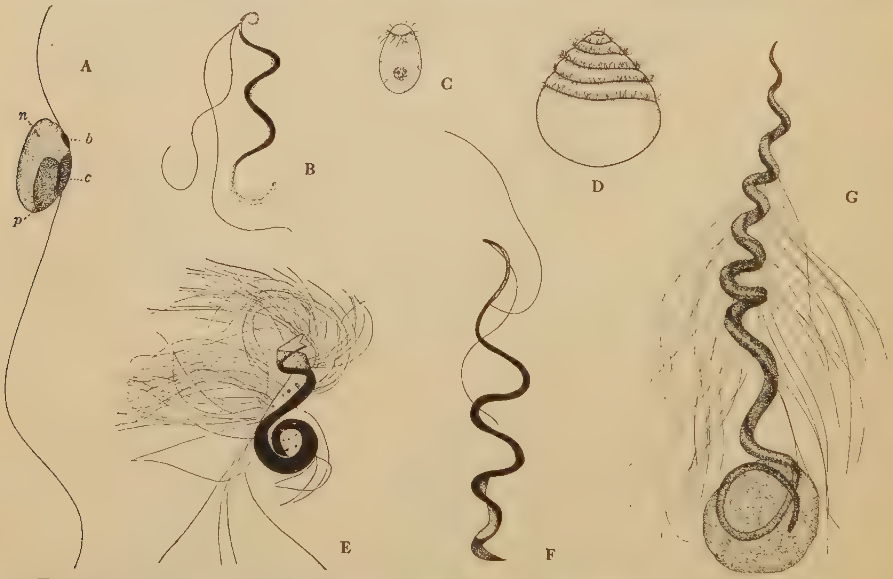

Fig. 132.—Spermatozoids of plants. *A*, *Fucus Areschougii; b*, blepharoplast; *c*, chromatophore; *n*, nucleus; *p*, plastomere. (*After Kylin*, 1920.) *B*, *Chara*. (*After Belajeff*.) *C*, *Œdogonium*. *D*, *Zamia*. (*After Webber*.) *E*, *Onoclea*. (*After Steil*, 1918*a*.) *F*, *Riccardia*. (*After Steil*, 1923.) *G*, *Marsilia;* spermatozoid extended as it enters gelatinous material about the archegonium; compare Fig. 138, *H*. (*After Sharp*, 1914.)

The mature spermatozoid in the algæ, like the zoöspore, is practically always described as a cytoplasmic body containing a nucleus, a motor apparatus, and an eyespot (plastid), with or without other plastids. The proportion represented by the nucleus apparently varies considerably, even within a genus. In *Fucus serratus*, for example, the figures of Guignard

(1889) and Kylin (1916) represent the cytoplasm as equaling or exceeding the nucleus in volume, whereas in *F. Areschougii* Kylin (1920) has shown that the main portion of the spermatozoid is nuclear, the cytoplasm being reduced to a very small amount (Fig. 132, *A*). At one side is the eyespot, which is derived from the chromatophore of the antheridial cell through an intermediate colorless stage. Connected with it is the blepharoplast, which arises from the centrioles, according to Meves (1918*c*). Farther back are one or more "plastomeres," which appear to be chondriosomal in nature.

**Bryophytes.**—The egg in bryophytes is the innermost cell of the axial row in the archegonium (Fig. 133). Commonly it enlarges, rounds up, and lies more or less free in the slimy fluid of the venter, the other axial cells meanwhile breaking down. In some genera (*Anthoceros, Sphagnum*) the ventral canal cell may also be organized as a functional egg, and there are other facts which suggest that the other cells of the axial row are also gametes historically. Besides a large nucleus, the egg contains a number of cytoplasmic bodies, among which are plastids and chondriosomes. In many cases a fairly distinct hyaline receptive spot is present at the side of the egg directed toward the neck of the archegonium.

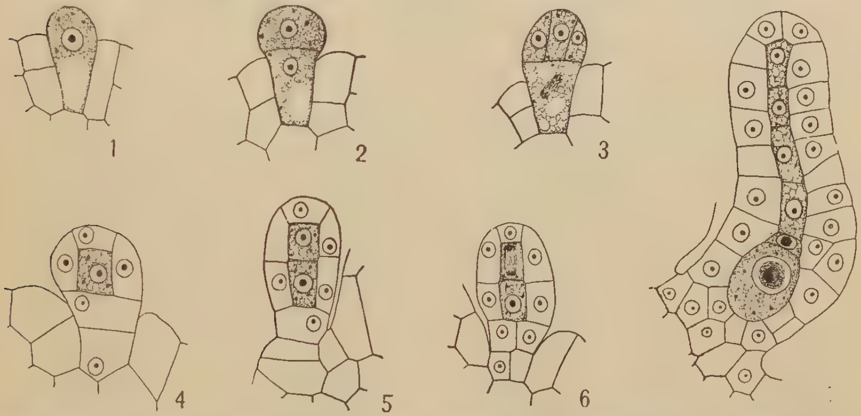

FIG. 133.—Successive stages in the development of the archegonium of *Reboulia*. In No. 7 are one egg, one ventral canal cell, and 4 neck canal cells. (*After Haupt*, 1921.)

Spermatogenesis in the bryophytes has been frequently studied.[1] In *Marchantia*, according to the account of Ikeno (1903), a minute centrosome comes out of the nucleus before each spermatogenous cell-division in the antheridium and divides into two; these pass to opposite sides of the cell and occupy the spindle poles during mitosis. After the last (diagonal) cell-division the centrosome passes to the plasma membrane at one corner of the cell (spermatid) and there elongates to form the blepharoplast, from which two long cilia grow out (Fig. 134). Meanwhile the nucleus becomes altered in shape, and forms the main portion of the body of the spermatozoid. In the cytoplasm of the spermatid is another structure, the "chromatoider Nebenkörper," which may possibly bear some relation to the small connecting piece seen later between the blepharoplast and nucleus. The process in the several other genera of liverworts so far investigated appears to be essentially the same, but in most of them centrosomes have been seen only during the last mitosis; in some cases such bodies are reported to appear first in the spermatids themselves. The blepharoplast in the spermatid of *Blasia* is of interest in that it divides into fragments which later reunite

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[1] Ikeno (1903), Miyake (1905*b*), C. E. Lewis (1906), Escoyez (1907*b*), Schaffner (1908), M. Wilson (1911), Woodburn (1911, 1913, 1915), C. E. Allen (1912, 1917*a*), Sharp (1920).

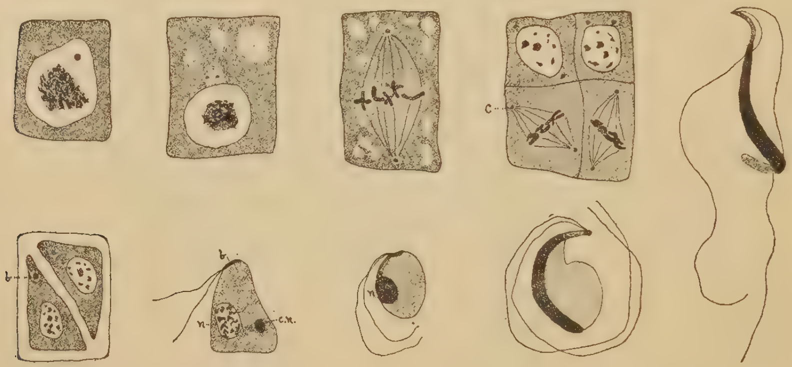

Fig. 134.—Spermatogenesis in *Marchantia*. *b*, blepharoplast; *c*, centrosome; *c.n.*, "chromatoider Nebenkörper;" *n*, nucleus. (*After Ikeno*, 1903.)

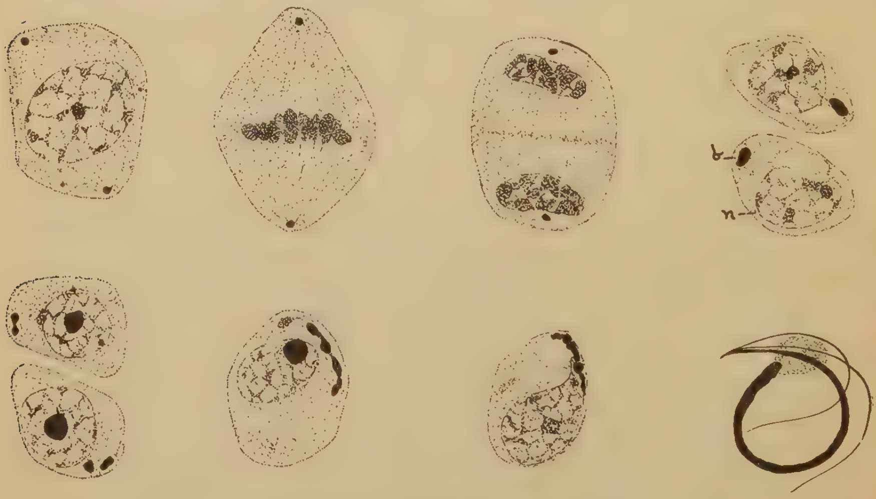

Fig. 135.—Spermatogenesis in *Blasia*. (*After Sharp*, 1920.)

to form the cilia-bearing rod, as is the case in certain vascular plants (Fig. 135) (Sharp, 1920). In the large spermatozoid of *Riccardia pinguis* Steil (1923) finds that the two cilia are unequal in length and are attached at different points (Fig. 132, *F*). Apparently, plastids are never present in the male gametes of plants above the algæ.

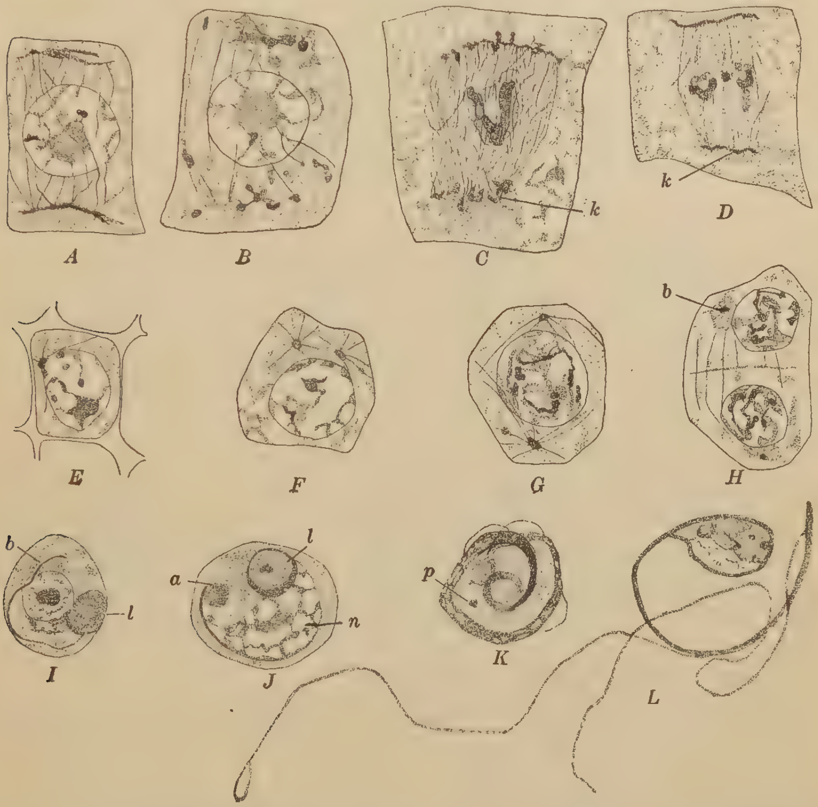

FIG. 136.—Spermatogenesis in *Polytrichum*. *A–D*, androgones, showing behavior of kinoplasmic plates and kinetosomes (*k*) during mitosis. *E–G*, androcyte mother-cells, showing division of central body. *H*, telophase of last mitosis; each androcyte has a blepharoplast (*b*). *I–K*, stages of transformation of androcyte into spermatozoid: *a*, apical body; *l*, limosphere; *n*, nucleus; *p*, percnosome. *L*, mature biciliate spermatozoid. (After *C. E. Allen*, 1912, 1917.)

The most detailed and critical of all researches on spermatogenesis in bryophytes are those of C. E. Allen (1912, 1917) on the moss, *Polytrichum juniperinum* (Fig. 136). The cytological phenomena accompanying the multiplication of the spermatogenous cells (*androgones*) up through the last mitosis, which differentiates the spermatids (*androcytes*), are briefly as follows. In the cytoplasm of all the androgones there is a deeply staining kinoplasmic mass; in the early androgones this has the form of a flat plate, while in the later ones it consists of a group of granules (kinetosomes). Prior to each mitosis the plate or group divides to daughter plates or groups which pass to the daughter cells. In each cell of the penultimate generation (androcyte mother-cell) there are no kinetosomes, but instead a spherical "central body" with radiations. This body divides into two which move apart and occupy the spindle poles during the last mitosis. Each resulting androcyte therefore has one such body, which functions as the blepharoplast. Allen does not regard the kinetosomes as definite morphological entities, but rather as masses of reserve kinoplasm. The blepharoplast, however, is a definite cell organ, with a problematic relation to the centrosome.

As the transformation of the androcyte (spermatid) into the spermatozoid begins, the blepharoplast elongates to form a uniform rod, and develops two cilia from near its anterior end. The nucleus moves against the middle portion of the blepharoplast, and the two elongate together in close union to form the body of the spermatozoid, the blepharoplast projecting beyond the anterior end of the nucleus. At about the time the blepharoplast begins to elongate a *limosphere* appears in the cytoplasm and takes up a position near the anterior end of the blepharoplast. Here it divides, giving rise to a small *apical body* that remains visible at the end of the blepharoplast until a comparatively late stage. The remaining portion of the limosphere may be seen lying against the nucleus until the maturity of the spermatozoid. Another body, the *percnosome*, is also seen in the cytoplasm at certain stages. In the opinion of Allen, the limosphere is probably identical with the "chromatoider Nebenkörper" described by Ikeno in *Marchantia*, and the percnosome with what M. Wilson (1911) termed the "accessory body." The apical body is here described for the first time by Allen.

It will be noted that the behavior of the limosphere and apical body in the moss shows a striking parallelism with that of the acroblast (Golgi material) and acrosome in animals, as subsequently described by Bowen (p. 311). Future researches on the spermatozoids of plants will be of much interest with reference to this point.

**Pteridophytes.**—In pteridophytes, as in bryophytes, the egg is the innermost cell of the axial row of the archegonium. The cytological characters of the egg appear to be much like those in the bryophytes. Often the egg is markedly flattened, or even concave on the receptive side, at the time of syngamy (Fig. 157).

There have been many researches on spermatogenesis in pteridophytes.[1] Our more definite knowledge of the subject began with the later researches of Belajeff (1897). The spermatozoids of all pteriodophytes, except *Lycopodium*, *Phylloglossum*, and *Selaginella*, differ from those of the bryophytes in having many cilia and usually a large number of spiral turns of the body. In the case of ordinary ferns, most of the accounts state that the blepharoplasts appear first either in the spermatids, or as centrosomes during the division which differentiates the spermatids. In *Equisetum* (Fig. 137) it has been shown that the blepharoplast appears as a functional centrosome in each cell of the penultimate generation; there it divides to two, which separate and establish between them the achromatic figure after the manner of animal centrosomes. At the close of mitosis the blepharoplast in each spermatid fragments into a number of pieces; these later join to form a continuous beaded thread from which the cilia grow out. In *Equisetum* the elongating nucleus and blepharoplast do not become closely joined as in other pteridophytes, but are held together only by the rather abundant cytoplasm.

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[1] Buchtien (1887), Campbell (1887), Belajeff (1888, 1897, 1898, 1899), Guignard (1889), Schottländer (1893), Shaw (1898*a*), Thom (1899), Yamanouchi (1908*b*), R. F. Allen (1911), Sharp (1912, 1914).

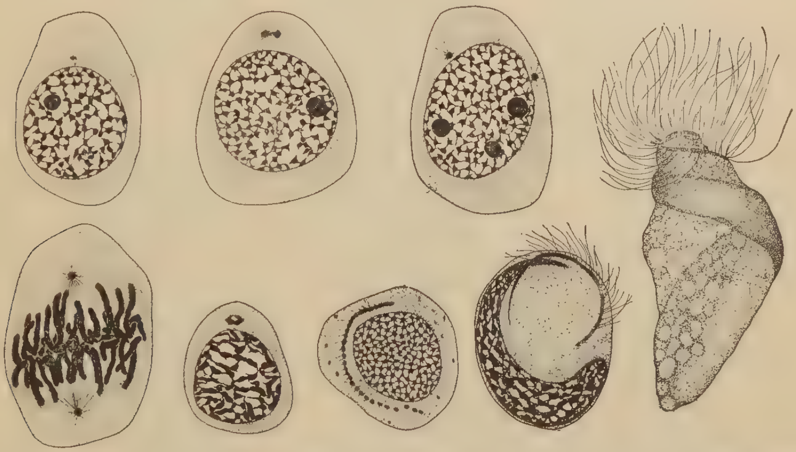

Fig. 137.—Spermatogenesis in *Equisetum arvense*, showing the behavior of the blepharoplast (centrosome) in the last spermatogenous mitosis and in the transformation of the spermatid into the spermatozoid. (*After Sharp*, 1912.)

The case of *Marsilia* is particularly interesting (Fig. 138). In this genus each of the two primary spermatogenous cells undergoes a series of four divisions which result in 16 spermatids. No distinct centrosomes appear during the first mitosis. During the anaphase of the second mitosis centrosomes develop at the spindle poles. During the telophase they divide, but are usually then resorbed in the cytoplasm. In the third mitosis centrosomes again develop at the spindle poles during the anaphase, and in the telophase they divide. The daughter centrosomes so formed then move apart and occupy the poles of the spindle through the fourth, or final mitosis. They are at all times accompanied by distinct cytoplasmic radiations, the achromatic figure being strikingly like those in thallophytes with centrosomes and in animals. Before the last mitosis is completed the centrosome (blepharoplast) becomes vacuolate, and in the spermatid it breaks up into a number of fragments; these later join to form a cilia-bearing band which elongates spirally in close union with the nucleus to form the spermatozoid.

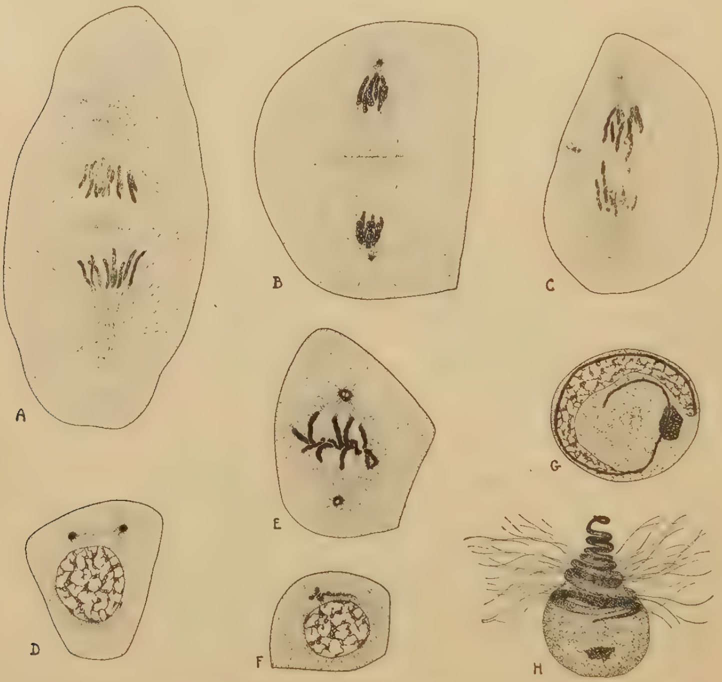

Fig. 138.—Spermatogenesis in *Marsilia quadrifolia*. *A*, first spermatogenous mitosis; no centrosomes. *B*, second mitosis; centrosomes present. *C*, third mitosis; centrosomes present; old centrosome divided and degenerating in cytoplasm. *D*, penultimate spermatogenous cell; daughter centrosomes separating. *E*, last (fourth) spermatogenous mitosis; blepharoplasts becoming vacuolate. *F*, fragmentation of blepharoplast in spermatid. *G*, transformation of spermatid into spermatozoid. *H*, free swimming spermatozoid. (*After Sharp*, 1914.)

**Gymnosperms.**—The eggs of gymnosperms[1] are among the largest of plant cells, the nucleus alone in certain cycads being more than a half-millimeter in diameter. Each egg is borne in an imbedded archegonium which has no neck canal cells, and only an evanescent ventral canal cell or nucleus (Fig. 139). The cells about the egg show a distinctly visible differentiation in connection with their nutritive function, and the egg is in close communication with them through large pits in the intervening walls. In most cases these pits are said to be closed by a membrane, the only direct connection being through minute plasmodesma. In *Dioön*, however, Chamberlain has shown that the membrane at first separating the projecting egg haustorium eventually ruptures, the cytoplasm of the egg and nutritive jacket cells becoming continuous. In the cycads the egg cytoplasm appears relatively free from conspicuous nutritive inclusions, but in conifers, such as *Pinus* or *Agathis*, there are large masses of proteinaceous ergastic material and other substances of uncertain origin and composition. The nucleus of the gymnosperm egg presents a peculiar appearance, being a large clear vesicle with masses of chromatic matter scattered about within it, apparently without the regularity of arrangement seen in other nuclei. Further studies are needed on this difficult subject.

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[1] Goroschankin (1883), Ikeno (1898), Chamberlain (1899, 1906, 1910, 1912, 1916), I. Smith (1904), Ferguson (1904), Stopes and Fujii (1906), and others. For a general account of gametogenesis in gymnosperms, with literature, see Coulter and Chamberlain (1910).

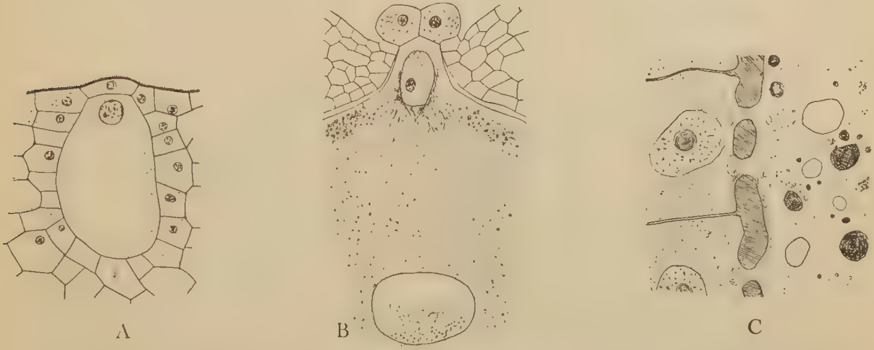

FIG. 139.—Oögenesis in *Dioön edule*. *A*, young archegonium. *B*, egg nucleus below and ventral canal nucleus above; two conspicuous neck cells. *C*, protrusions of the egg cytoplasm (at right) extending as haustoria through pores in the egg membrane into the surrounding jacket cells (at left). (*After Chamberlain*, 1906.)

In the gymnosperms there are two principal types of spermatogenesis, some of the orders (Cycadales, Ginkgoales) having ciliated spermatozoids, and the others (Coniferales, Gnetales) non-motile male cells. In most cycads and *Ginkgo* a greatly enlarged "body-cell" in the developing pollen tube gives rise to two spermatozoids by a process which is essentially as follows.[1] In the cytoplasm of the body-cell are numerous minute "black granules" of uncertain origin (Chamberlain on *Dioön*) (Fig. 140). Two blepharoplasts now develop, apparently by the enlargement of two of the black granules, and take up positions on opposite sides of the nucleus. Very conspicuous radiations appear about them. The body-cell now divides; the mitotic figure is wholly intranuclear, and although the blepharoplasts remain opposite its poles they appear to have no direct connection with it. A wall appears between the two daughter nuclei at the close of mitosis, and in each of the resulting cells a spermatozoid is organized. Even before the division of the body-cell nucleus the bleph-

[1] Hirasé (1894), Ikeno (1898), Fujii (1898, 1899), Webber (1897, 1901), Caldwell (1907), Miyake (1906), Chamberlain (1909, 1916).

aroplasts, which have become very large, are seen to be vacuolate. After the division is completed each of them breaks up into a number of small fragments which then coalesce and begin the formation of the spirally coiled band that bears the many cilia. This band, or blepharoplast, continues to elongate just within the cell membrane, a prolongation of the nucleus being in contact with its growing end; eventually it makes several turns. The mature spermatozoid consists of an enormous nucleus, which in the living condition can be seen to undergo amœboid changes of

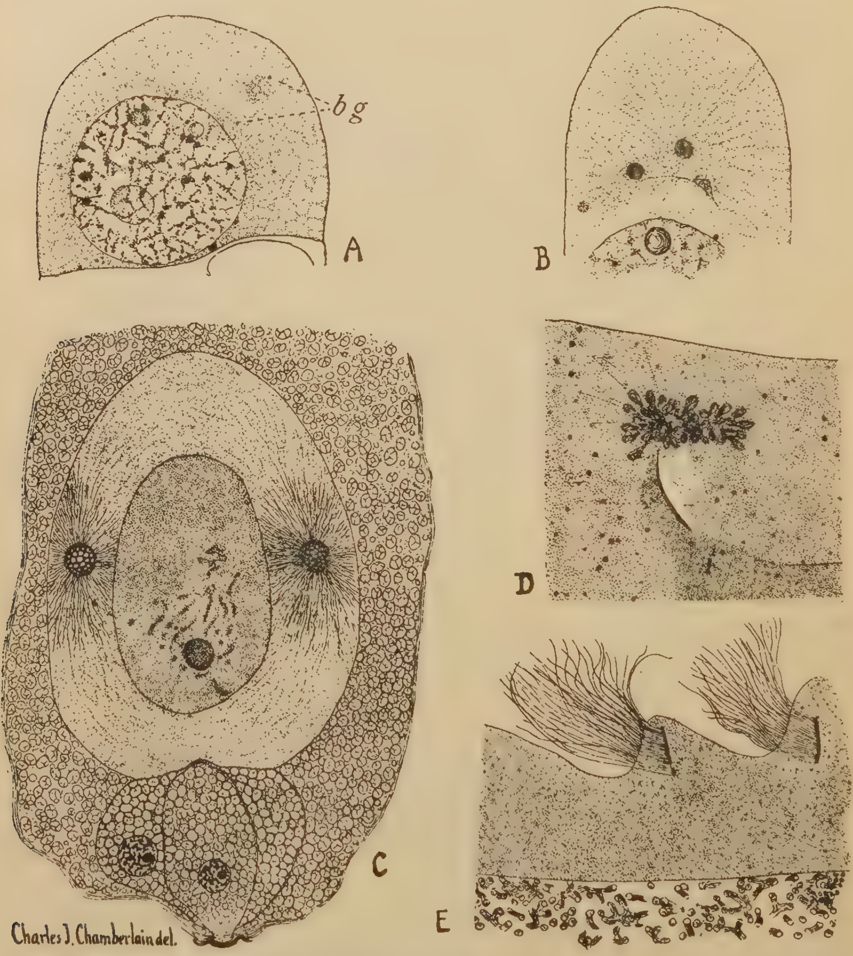

Fig. 140.—Stages in spermatogenesis in *Dioön edule*. *A*, "body-cell," with black granules in cytoplasm. *B*, two blepharoplasts differentiated. *C*, body-cell with two blepharoplasts; prothallial and stalk cells below. *D*, fragmentation of blepharoplast in spermatid as spiral band begins to form. *E*, portion of edge of section of spermatozoid, showing spiral blepharoplast cut at two points and cilia growing from it. (*After Chamberlain*, 1909.)

shape, a cytoplasmic sheath, and the spiral blepharoplast with its many cilia.

In the conifers, as in the cycads, the body-cell divides to form two male gametes, but here they are non-motile. In some genera (*Taxodium*) a wall separates the two nuclei after mitosis in the body-cell, but in others (*Pinus*) these nuclei lie together in the body-cell cytoplasm. As the body-cell moves down the pollen tube its outlines may remain distinct, but in some cases its cytoplasm becomes intermingled with that of the pollen tube; in the latter event the male gametes are simply nuclei rather than complete cells. In some genera the two male gametes are differentiated in size and apparently in function, a tendency which reaches its extreme expression in the Podocarpineæ. Although some vestige of blepharoplasts might be expected in the male cells of conifers, none has been identified. The further history of the gametes will be followed in the next chapter.

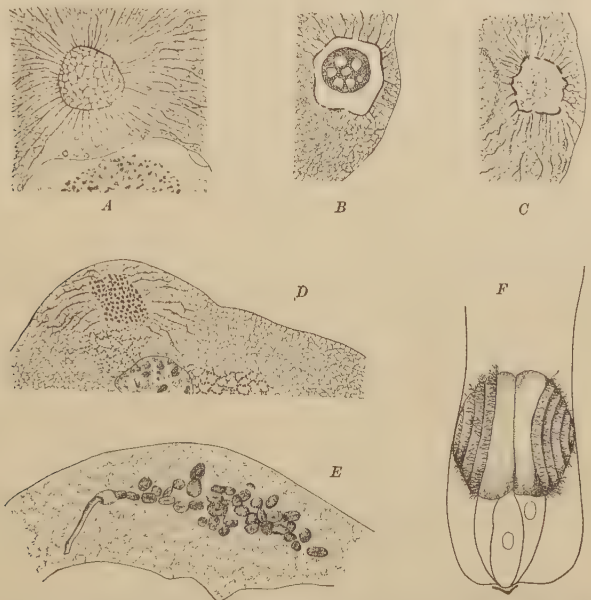

FIG. 141.—*A–E*, five stages in the vacuolation and fragmentation of the blepharoplast during the mitosis differentiating the spermatids in *Zamia*. *F*, the two spermatozoids in end of pollen tube; prothallial and stalk cells below them. (*After Webber*, 1901.)

**The Homology of the Blepharoplast.**—The theory that the blepharoplast is actually homologous with the centrosome, which it so strikingly resembles, was originally suggested by Belajeff (1897) and strongly advocated by Ikeno (1898, 1904, 1906). Various objections have been brought against this interpretation (Webber, Shaw, Woodburn), but subsequent researches on both plants and animals have sustained it. Ikeno, although at first inclined to regard all blepharoplasts as homologous, later separated them into three categories: centrosomal blepharoplasts (myxomycetes, bryophytes, pteridophytes, gymnosperms); plasmodermal blepharoplasts (green algæ); and nuclear blepharoplasts (certain flagellates). A survey of the centrosomal blepharoplasts through the various groups in which they occur shows that centrosomes functioning in the ordinary way through several mitoses gradually become restricted to one, their original rôle becoming less evident as they become modified in connection with their additional function, the bearing of cilia. The situation may be summed up as follows (Sharp, 1912):[1]

> Although limited to a single mitosis in the antheridium, the blepharoplast [of *Equisetum*] retains in its activities the most unmistakable evidences of a centrosome nature, and at the same time shows a metamorphosis strikingly like that in the cycads. In thus combining the main characteristics of true centrosomes with the peculiar features of the most advanced blepharoplasts, it reveals in its ontogeny an outline of the phylogeny of the blepharoplast as it is seen developing through bryophytes, pteridophytes, and gymnosperms, from a functional centrosome to a highly differentiated cilia-bearing organ with very few centrosome resemblances.
>
> The activities of the blepharoplast in *Equisetum* [*Marsilia* and *Blasia*], taken together with the behavior of recognized true centrosomes in plants and analogous phenomena in animals, are believed to constitute conclusive evidence in favor of the theory that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes.

**Angiosperms.**—Gametogenesis in angiosperms has already been touched upon in the preceding chapter (see Figs. 106 and 107). The microspore nucleus divides equationally, giving rise to a generative cell; this is usually smaller than the tube-cell, from which it is separated by a delicate membrane. The generative cell divides to form the two male cells; this division sometimes occurs in the pollen grain before shedding, as in Fig. 106, but apparently more often in the growing pollen tube after pollination. The membranes bounding the male cells may disappear, leaving the two male nuclei free in the common cytoplasm of the pollen grain or tube (Schürhoff, 1919*b*). In other cases it has been shown that they remain intact until the surface of the egg is reached (*e.g.*, Wylie on *Vallisneria*, 1923). At first the male nuclei are similar to other nuclei in appearance, but in many plants they become vermiform, particularly after entering the embryo sac (Fig. 161, *D*, *E*).[2] This shape may be maintained up to the time of fusion, but in other instances it later gives way to the ordinary shape (*Fritillaria;* Sax, 1916). This change may occur more rapidly in one male nucleus than in the other, the two thus being unlike at late stages. It has frequently been suggested that vermiform male nuclei have a special power of independent movement, though, of course, no blepharoplasts or cilia are present in the angiosperms.

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[1] See also the discussions of Ikeno (1904, 1906), Chamberlain (1898), and Guignard (1898).

[2] Mottier (1898*a*), Nawaschin (1899, 1900, 1909, 1910), Guignard (1900), Blackman and Welsford (1913), Welsford (1914), Sax (1916, 1918).

The nucleus of the functional megaspore initiates a series of three equational divisions, the resulting eight nuclei lying free in the common cytoplasm of the embryo sac (Fig. 107). Ordinarily three nuclei remain in each end of the sac while the other two (*polar nuclei*) meet and fuse sooner or later. Thin membranes are now differentiated in the cytoplasm between the nuclei in the ends of the sac, giving a group of three *antipodal cells* in the chalazal end, and an *egg* and two *synergids* in the micropylar end. The angiosperm egg usually shows very little special morphological differentiation, and except for its size and the position of its nucleus and vacuoles it closely resembles the synergids; in fact, cases are known in which synergids as well as eggs may develop into embryos. Commonly, the egg is somewhat larger than the other cells, carries its nucleus in the end towards the center of the sac, and has one or more large vacuoles. Visible ergastic materials other than cell sap are usually not conspicuous. Chondriosomes and plastids in some form are probably present regularly. The egg, like the male gamete, contains the reduced number of chromosomes, and although its nucleus is ordinarily removed from the immediate product of meiosis by three mitoses, cases are known in which its differentiation follows meiosis even more closely (p. 248).

**Oögenesis in Animals.**—The primordial germ cells in animals, whatever the time and place of their origin may be, are eventually found in definite germ glands, the ovaries and testes. When first distinguishable the female germ cell is small and relatively undifferentiated (Fig. 142), but in the ovary it passes through a "growth period," during which it not only becomes greatly enlarged and stocked with reserve food substances (yolk), but often develops visibly differentiated regions which may bear a direct relation to the embryonic parts which arise later (Fig. 187). This growth and differentiation of the oöcyte[1] prior to meiosis and syngamy often involves the activity of a special follicular epithelium organized about it, and also in some instances a distinct group of "nurse cells" (Fig. 210). The nucleus of the oöcyte is known as the "germinal vesicle," and passes through the growth period in a stage of the first meiotic prophase. After the oöcyte has nearly or quite reached its full size, even after the spermatozoön has entered in many cases, its nucleus undergoes the meiotic mitoses in rapid succession, the resulting polar bodies being budded off as separate cells or retained within the egg to be resorbed later (Figs. 165; 210, *3*). The nucleus of the "matured" egg normally retains the haploid number of chromosomes. Especially noteworthy in connection with certain theoretical problems is the high degree of structural

[1] See Hegner (1914) and Wilson (1925).

differentiation reached in many animal eggs before syngamy: the development of the new individual of the next generation actually begins before this event, or even before meiosis.

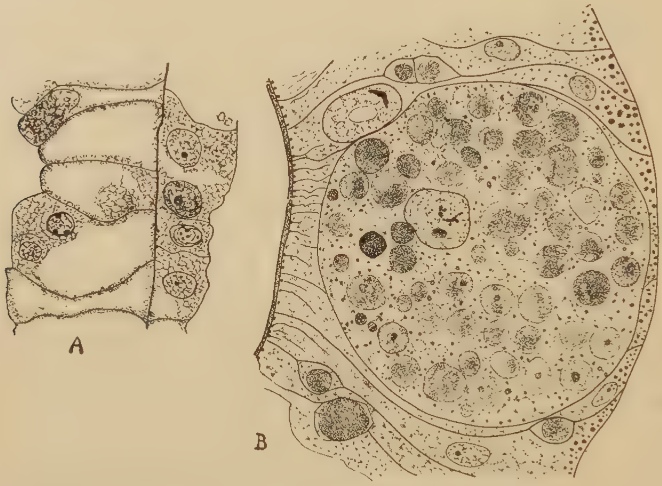

Fig. 142.—The differentiation of the oöcyte in *Hydra*. *A*, very young oöcyte lying between ectodermal cells at right. *B*, oöcyte after growth period, with yolk globules. (*After Downing*, 1909.)

**Spermatogenesis in Animals.**—The development of the spermatozoön has long been one of the most fascinating and difficult problems in cytology. The several components of the germ cell undergo an astonishingly complicated series of transformations, and these, together with the types of spermatozoa resulting, differ considerably in detail from group to group. This has naturally led to much confusion in the literature on the subject, although many points were well covered by the early investigations. The recent outstanding researches of Bowen (1920–1924) have so clarified our conceptions with regard to many previously obscure points that his descriptions will be used as the principal basis of the following account.[1] Bowen worked chiefly with insects (Hemiptera, Orthoptera, Lepidoptera, Coleoptera, Aptera) and amphibia (*Plethodon*), but comparisons show that his descriptions, with minor modifications, will apply to the general features of spermatogenesis in various other groups.

Reference has been made (p. 240) to the multiplication of the early male germ cells (spermatogonia) in the testis, their enlargement to form spermatocytes, and the reduction of the chromosomes in the two mitoses occurring as each spermatocyte divides into four spermatids, which then become transformed into four spermatozoa. We shall begin the present description with the spermatocyte, and follow its various components through the meiotic divisions, and then through the metamorphosis of the spermatid.

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[1] The author is indebted to Dr. Bowen for the loan of his original drawings. For further general accounts of animal spermatogenesis, see Wilson (1925), and the résumé by Bowen (1924*c*).

*The Spermatocyte and Its Divisions* (Fig. 143).—In the spermatocyte are the following components: nucleus, cytoplasm, chondriosomes, Golgi material, a pair (usually) of centrioles, and frequently other formed elements of questionable nature. The nucleus is relatively large, and usually passes the growth period in a stage of the prophase of the first meiotic mitosis. The chondriosomes are present in the form of granules, rods, or threads; and although they behave variously in different species, they are usually distributed rather equally to the four spermatids in the meiotic divisions. This in some cases involves the passive division of individual chondriosomal threads (Fig. 35), or an even more precise distribution (Fig. 36). The centrioles diverge to opposite sides of the cell and occupy the foci of the achromatic figure in each mitosis. At the close of the second mitosis the centriole usually divides, so that the spermatid has a pair of them. Much confusion in terminology and diversity of interpretation have arisen concerning the special differentiations which may occur about the centrioles, and the topographic relation

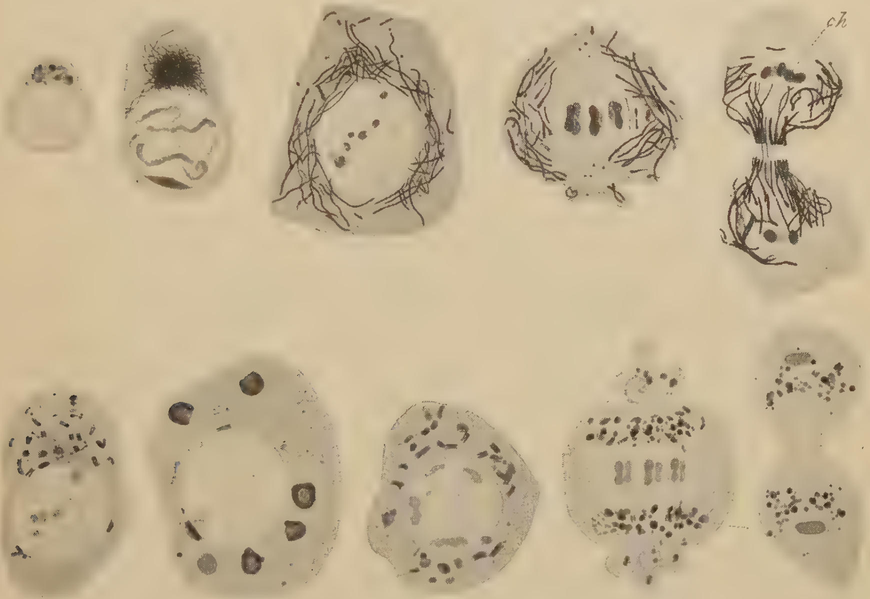

FIG. 143.—The first division of the spermatocyte of *Euschistus*, showing the behavior of the chondriosomes (first row) and the Golgi material (second row). *ch*, chromsomes. (*After Bowen*, 1920.)

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which certain other cell components, notably the Golgi material, may bear to them at certain stages.

Two general modes of arrangement of Golgi material in spermatocytes may be distinguished. In the insects (Bowen) a number of Golgi bodies, each composed of two substances differing in the intensity with which they stain, are scattered throughout the cytoplasm. At each of the meiotic divisions they break up into fragments (dictyosomes; see p. 132), which become arranged around the nucleus at the equator of the cell and pass as equal groups to the two poles in advance of the chromosomes. It is probable that in some cases each Golgi body does not divide (Gatenby). In another series of forms (mollusks, amphibia, other vertebrates) the Golgi bodies are closely aggregated about the centrioles, where their lightly staining substance flows together to form the *idiosome* (designated by other terms also), while their deeply staining constituent remains as separate chromatic rodlets adhering to the surface of the idio-

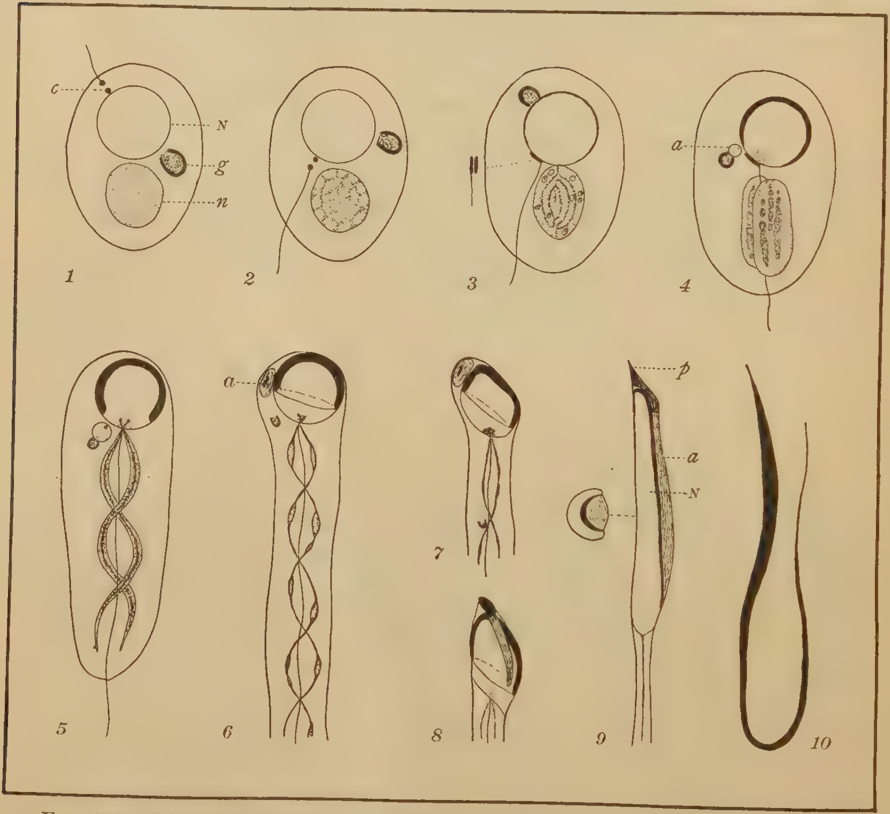

FIG. 144.—Diagram illustrating the principal features of spermiogenesis in animals as shown in the following figures from Bowen. *a*, acrosome; *c*, centrioles; *g*, Golgi material (acroblast); *N*, nucleus; *n*, nebenkern; *p*, perforatorium. (*Based on the diagrams and other figures of Bowen.*)

some. This chromatic matter often appears as a network or a continuous shell instead of separate rodlets, but it is uncertain how far such appearances are due to the action of fixatives. It was formerly thought that the idiosome substance was related primarily to the centrioles, the Golgi material collecting about it at certain stages, but the situation in insects seems to show that the real unit is the Golgi body composed of chromatic "Golgi matter" and relatively achromatic "idiosome substance," a close topographic relation to the centrioles being assumed only in certain cases. In the meiotic divisions the chromatic Golgi rodlets (or network or shell) form a number of dictyosomes which pass as two groups to the poles; whether each divides or not is a question. The fate of the idiosome substance is difficult to determine, but Bowen thinks it probable that each dictyosome is a minute Golgi body with its two substances, which are thus distributed to the four spermatids. In *Gryllotalpa,* according to Voïnov (1925), there is a single large Golgi body or dictyosome in the spermatocyte. This divides to form four, which are distributed to the spermatids.

At the close of the meiotic divisions each spermatid consists of cytoplasm, a nucleus with the haploid number of chromosomes, some chondriosomes, a pair of centrioles, a number (usually) of Golgi bodies, and often ergastic inclusions. These various elements will now be followed through the metamorphosis of the spermatid into a spermatozoön (*spermiogenesis*). The essential changes are shown diagrammatically in Fig. 144 and in detail in Figs. 145–148.

*The Centrioles.*—In the Hemiptera (Bowen) the two centrioles are situated near the anterior end of the young spermatid, one of them lying in contact with the nuclear membrane. From the distal member of the pair the delicate axial filament of the flagellum grows out and pierces the cell membrane. In many insects this filament may appear much earlier, before mitosis is complete or even in the primary spermatocyte (moths). The centrioles now migrate to a position near the posterior pole of the nucleus, where they take the form of parallel rods lying against the nuclear membrane, and soon form a V, with the elongating axial filament extending from its angle. An intranuclear body ("pseudoblepharoplast") present during these stages has often been confused with the centrioles. The centrioles eventually constitute the so-called "centrosomal middle piece" at the base of the sperm head, but in insects this is not a very distinct structure.

The centrioles in certain other animals show curious modifications into rings and knob-like structures which have been variously interpreted. In his early accounts of spermatogenesis in the salamander Meves (1896, 1897) reported that the distal centriole, after the appearance of the axial filament, transformed itself into a ring; the filament then passed through it and attached itself to the proximal centriole, which pushed into the base of the nucleus and enlarged to form the middle piece. Meanwhile the ring divided into two parts, one of which became the "end-knob" at the posterior end of the middle piece, while the other passed backward along the axial filament. In mammals (rat, man) Meves (1898, 1899) found much the same situation: the proximal centriole remained near the nucleus and did not elongate to form a middle piece. The distal centriole then divided, one part forming the end-knob and the other passing back as a ring to the end of the "connecting piece," which does not correspond to the middle piece of the salamander. In *Œcanthus nigricornis,* a cricket, Johnson (1922) states that the distal centriole, to which the axial filament is attached, constricts off a ring-shaped portion which encircles the filament and works backward along it to the end of the tail sheath, while the remaining portion, bearing the filament, comes to lie very close to the proximal centriole.

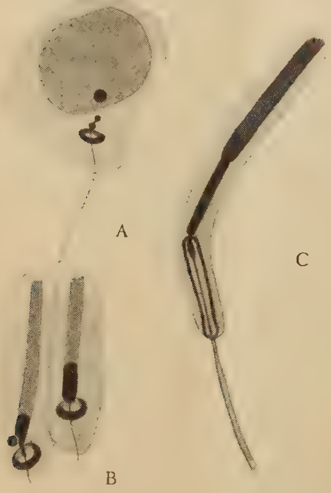

FIG. 145.—The behavior of the centrioles in the spermiogenesis of *Plethodon cinereus.* *A*, spermatid with divided proximal (?) centriole. *B*, later stage; one portion of the proximal (?) centriole has fused with the posterior end of the middle piece. *C*, subsequent elongation of the ring-shaped centriole. (*After Bowen,* 1922*a*.)

*The Chondriosomes* (Fig. 146).—In insects generally the chondriosomes flow together to form a single more or less compact body, the *nebenkern* (the *mitosome* of Gatenby).[1] This nebenkern soon shows a very complex structure. Vacuoles of a lightly staining fluid appear within it, chiefly near its periphery (this simulates the "blackberry stage" reported after certain fixatives). Soon the more chromatic material takes the form of a series of concentric plates alternating with layers of the lighter substance (the "onion stage"). The platework now becomes simpler in structure, the chromatic plates taking the form of a hollow ovoid mass with a median partition. As the nebenkern elongates the ovoid mass shrinks, and as it does so a furrow follows it inward and eventually cuts the nebenkern in two as the chromatic mass vanishes. Meanwhile globules of an additional "central substance" appear in the light nebenkern matrix, arrange themselves in rows, and coalesce to form beaded strands. As the nebenkern halves elongate further these strands unite until each half finally has a single axial core composed of the central substance.

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[1] Since the term "nebenkern" has been used for other bodies, including the acroblast (Golgi material), many workers are ceasing to use it. We have here followed Bowen in retaining it provisionally for the chondriosomal body.

The nebenkern halves now come to lie on either side of the axial filament and rapidly elongate to form the two "filament sheaths" which become twisted about the axial filament. Their anterior ends appear to attach themselves to the centrioles at the base of the nucleus. As they become longer and thinner they show a series of bleb-like swellings which may possibly represent accumulations of the central substance; these eventually disappear and the uniform sheaths extend nearly, if not quite, to the tip of the axial filament. In the spermatozoön of *Ascaris*, which has no flagellum, the granular chondriosomes are carried in the rather abundant cytoplasm which surrounds the nucleus.

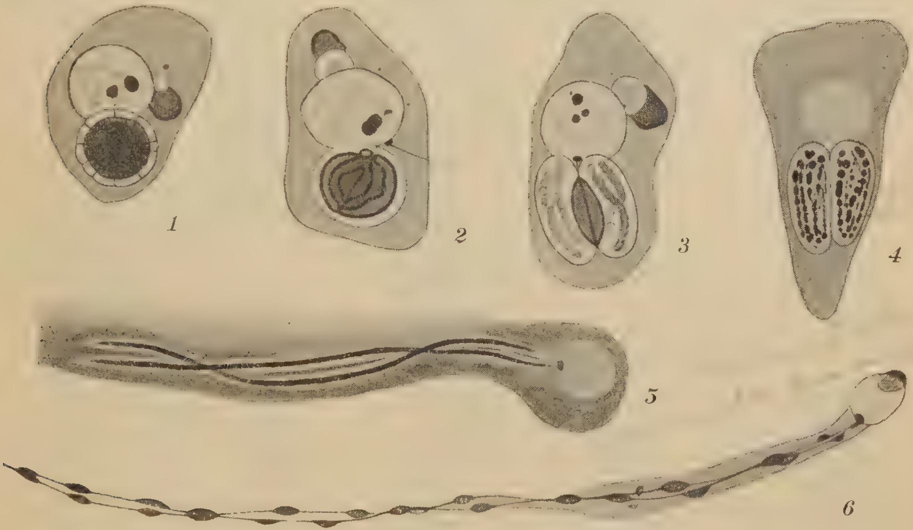

FIG. 146.—The transformation of the nebenkern in the spermiogenesis of *Brochymena*. Compare Fig. 144. (*After Bowen*, 1922*cd*.)

*The Golgi Material* (Fig. 147).—In the Hemiptera the Golgi constituents of the spermatid usually behave as follows. At the close of the meiotic divisions the dictyosomes fuse to form several larger Golgi bodies much like those of the spermatocyte. The fusion continues until there is formed a single large *acroblast*,[1] which lies near the base of the nucleus on the side opposite that to which the centrioles migrate. Ordinarily, it has a heavily staining shell except on the side next to the nucleus. The acroblast soon begins a migration around to the other side of the nucleus, passing first to the anterior end of the cell, where it pauses for a time. It then continues along the nuclear membrane on the other side, following the path of the centrioles, and eventually comes to lie near them.

[1] Often referred to in the literature as the "spermatid idiosome" or "sphere." In mollusks this mass has frequently been called the "nebenkern."

During the migration of the acroblast an *acrosome* is differentiated from it. This first appears as a delicate vesicle on the side of the acroblast next to the nucleus, and seems to consist of a new material, the formation of which is dependent upon the activity of the substance of the acroblast. Within it is a small granule. Very rarely the acrosome itself has the form of a granule rather than a vesicle (mollusks, Gatenby; grasshopper, Bowen). The acroblast becomes somewhat smaller as the acrosome grows, and together they move again toward the anterior end of the cell. Either before or after reaching the apex they separate from each other, the acrosome taking its final position near the apex while the remainder of the acroblast, known as the "Golgi remnant," passes backward along the tail and is ultimately cast out of the cell in a protoplasmic ball sloughed off at the close of spermiogenesis.[1] In certain mammals a portion of the Golgi remnant is said to remain as a part of the middle piece (Weigl, 1912; Gatenby and Woodger, 1921). Attention may be called in passing to the suggestive similarity of the behavior of the acroblast and

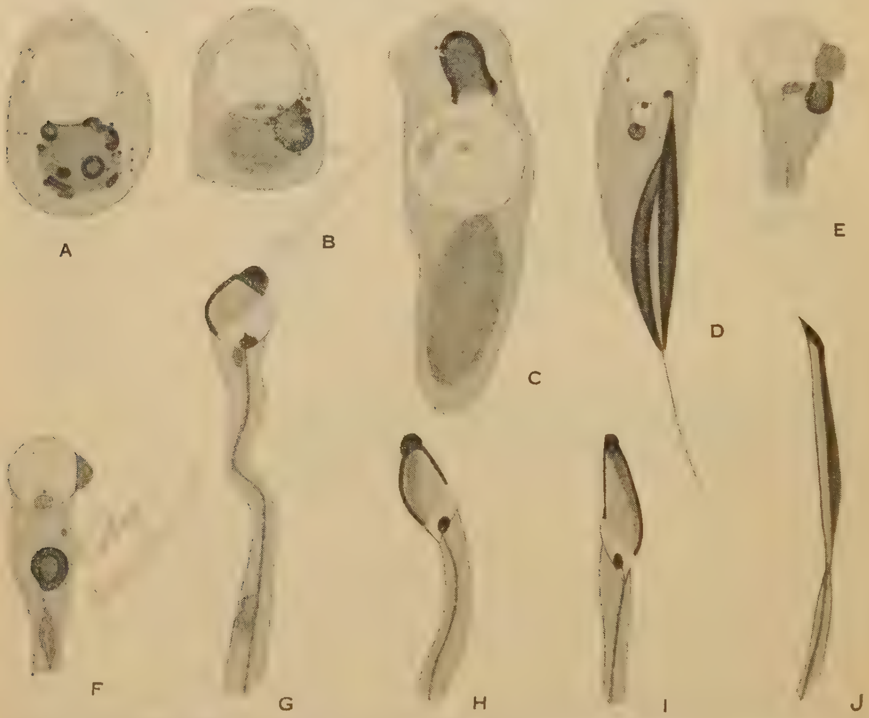

FIG. 147.—The behavior of the Golgi material in the spermiogenesis of certain insects. *A* and *F*, *Brochymena*; *B–E*, *Euschistus*; *G–J*, *Murgantia*. Compare Fig. 144. (*After Bowen*, 1920, 1922c.)

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[1] It appears to be so cast out in the guinea pig (Sjövall, 1906), *Geotriton* (Terni, 1914), mollusks and Lepidoptera (Gatenby, 1917).

acrosome to that of the limosphere and apical body in the moss, *Polytrichum juniperinum* (p. 298).

Another mode of acrosome formation occurs in certain Lepidoptera (*Pygæra*, *Callosamia*) and grasshoppers (*Rhomaleum*, *Dissosteira*), according to Bowen (1922*ac*) (Fig. 148). Here the Golgi bodies in the spermatid do not fuse to form a single acroblast, but remain as a small group. Just how these bodies give rise to the acrosome is not certainly known, but it seems probable that all of them contribute material to a common acrosome, each Golgi body acting thus as an acroblast. In the Lepidoptera the acrosome is of the usual vesicular type, whereas in the grasshoppers it has the form of a granule. In *Fasciolaria tulipa*, a gastropod, Hyman (1923) states that an acroblast formed by fusion of Golgi bodies breaks up into chromatic portions, one of which becomes a vesicular acrosome while the others are cast out.

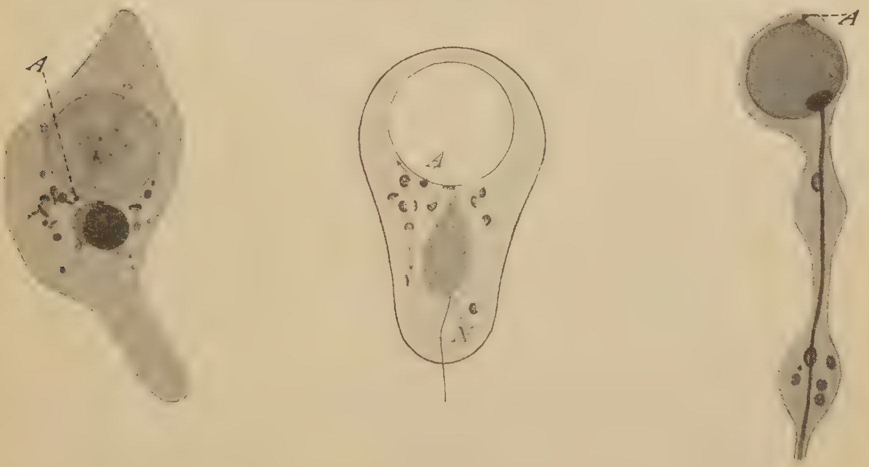

FIG. 148.—The behavior of the Golgi material in the spermiogenesis of *Rhomaleum*. *A*, acrosome; *N*, nebenkern. (*After Bowen*, 1922*ab*.)

The acrosome, after reaching its definitive position near the anterior end, undergoes a further differentiation. Within it appears a deeply staining mass which may possibly bear some relation to the granule observed in the vesicular acrosome at earlier stages. It rapidly develops into the pointed *perforatorium* at the tip of the spermatozoön, while the remaining portion of the acrosome grows backward as a band against one side of the asymmetrical and elongating nucleus, with which it becomes very intimately united as the spermatozoön matures. It is the view of Bowen (1924*b*) that the acrosome or perforatorium is not a boring organ, as commonly thought, but is rather a secretion with a special function in fertilization, thus corresponding in origin with the secretion droplets observed to arise in connection with the Golgi material in gland cells (Nassonow; Bowen).

Van Herwerden has shown the presence of an oxidase in the acrosome region. Certainly the acrosome cannot be a boring organ in the spermatozoön of *Lepisma,* in which it lies at the base of the nucleus rather than anterior to it (Bowen). In *Gryllotalpa,* according to Voïnov (1925), another cytoplasmic element, the "spherular apparatus," coöperates with the acrosome in forming the perforatorium.

*The Nucleus.*—No conspicuous changes occur within the nucleus until the acroblast and its differentiated acrosome have completed part or all of their migration around it. The chromatic substance is then seen to arrange itself in a layer against the inside of the nuclear membrane, and as spermiogenesis proceeds it abandons the posterior portion and collects as a compact, deeply staining cap at the anterior side. As the acrosome begins to form the perforatorium this chromatic cap becomes very asymmetrical, and the whole nucleus elongates and begins its transformation into the slender sperm head. The "pseudoblepharoplast," which has already been mentioned, and which may possibly represent chromosome material, disappears at about this stage. The head continues to elongate in the form of a narrow spoon with the acrosomic band lying in the hollow, and eventually becomes a slender pointed body in which nucleus and acrosome can no longer be distinguished. During these changes the non-chromatic constituents of the nucleus gradually diminish and disappear, so that the nucleus of the spermatozoön is an extremely concentrated chromatic mass in which any structure can be demonstrated only in very rare cases.

*The Cytoplasm.*—As the other components of the spermatid undergo the transformation outlined in the foregoing pages, the cytoplasmic cell body elongates and continues to surround them (with the possible exception of the tip of the axial filament) until a comparatively late stage. It may be supposed on theoretical grounds that some cytoplasmic material, if only a thin membrane, must be present even about the mature spermatozoön, but ordinarily such a membrane is not to be distinguished, especially in the head region. Koltzoff (1909), however, was able to demonstrate a membrane about the head by using hypotonic solutions. Toward the close of spermiogenesis in the insects it has been ascertained that a cytoplasmic ball, containing the Golgi remnant and other granules of an unknown nature, is sloughed off and ingested by the nutritive epithelial cells lining the spermatic cyst. In other animal groups, likewise, a cytoplasmic mass is similarly eliminated, but the amount of "active" protoplasm contained in these so-called "protoplasmic balls" is still a question.

*The Mature Spermatozoön.*—The mature flagellate spermatozoön comprises two main components: a *head,* which is made up of a solid homogeneous chromatic mass representing the nucleus, an acrosome, and sometimes a skeletal fiber of uncertain origin; and a *tail,* consisting of an

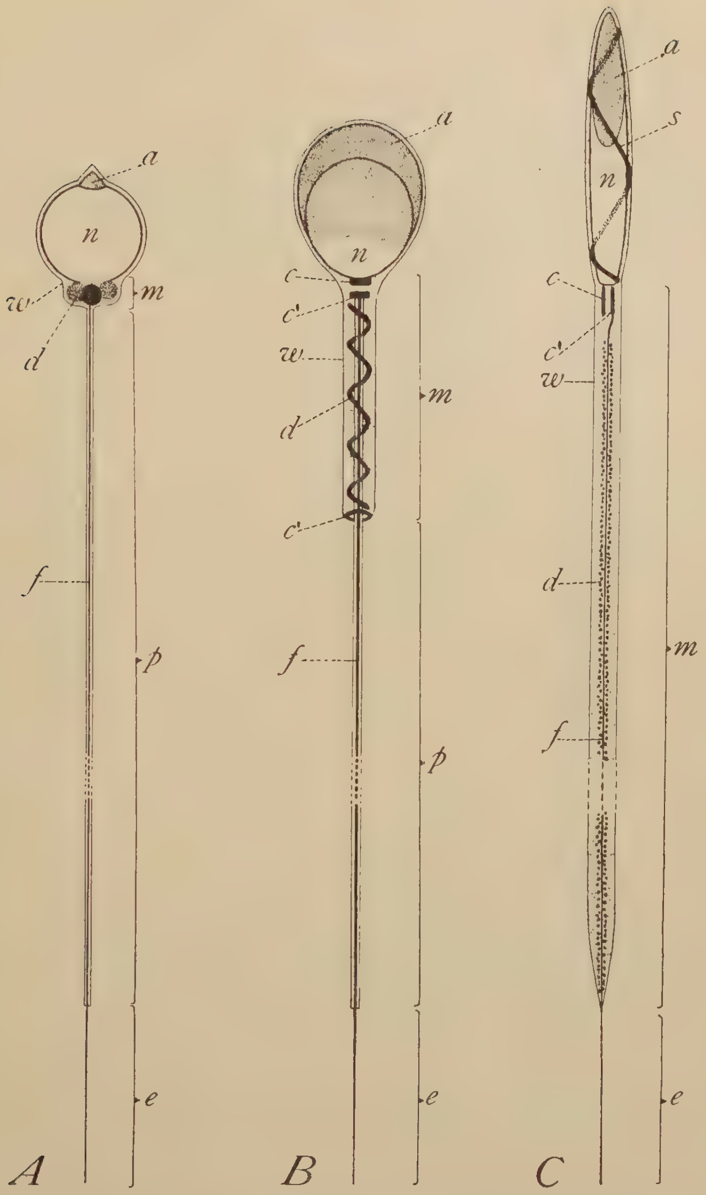

FIG. 149.—Diagrams of typical spermatozoa, particularly to illustrate various features in the development of the tail region. *A*, based on echinoderm, annelid, and mollusk; *B*, based on mammal; *C*, based largely on insect and mollusk—mitochondrial tail sheath represented in a schematized form. *a*, acrosome; *c*, proximal centriole; *c'*, distal centriole or its derivatives; *d*, mitochondria; *f*, tail or axial filament; *n*, nucleus; *s*, skeletal fiber in head; *w*, cell membrane; *m*, middle piece; *p*, principal piece; *e*, end piece. (*Figure and legend from Bowen*, 1924*c*.)

axial filament produced as an outgrowth from the distal centriole, the thread-like sheaths formed by the chondriosomal derivatives, and an uncertain amount of residual cytoplasm. In many animals, particularly mammals, a "middle piece" is more distinctly differentiated than it is in insects, the spermatozoön therefore appearing to have three main parts. In general, it is more convenient to think of the middle piece as a portion of the tail. The tail of the typical animal spermatozoön as a rule may thus be said to have three segments, though in certain animals all of them may not be differentiated. These three segments are the "middle piece," in which the axial filament is enclosed in a sheath of undifferentiated cytoplasm carrying the mitochondrial elements and the centrioles; a "principal piece," which has a thin sheath of questionable origin but no undifferentiated cytoplasm; and an "end piece," which is the naked posterior end of the axial filament. Diagrams of three common types of spermatozoa are shown in Fig. 149. Bowen holds it probable that the phenomena of spermatogenesis are essentially the same in all insects, and further that, at least so far as the principal changes undergone by the various cell elements are concerned, the process is fundamentally the same

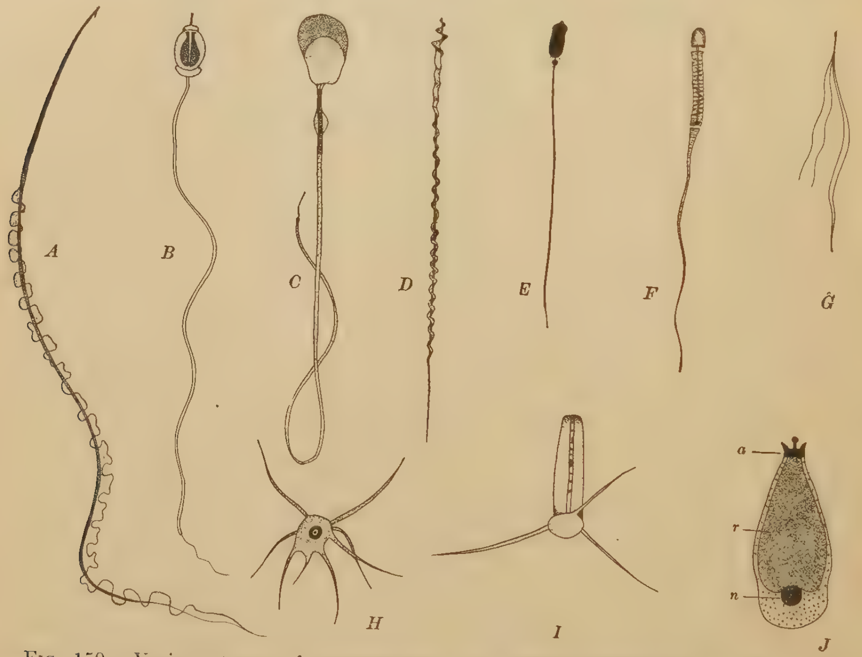

FIG. 150.—Various types of spermatozoa. *A*, *Triton* (salamander). (*After Ballowitz.*) *B*, *Nereis* (annelid). (*After F. R. Lillie.*) *C*, guinea pig. (*After Meves.*) *D*, *Phyllopneuste* (bird). (*After Ballowitz.*) *E*, sturgeon. (*After Ballowitz.*) *F*, *Vesperugo* (bat). (*After Ballowitz.*) *G*, *Castrada* (turbellarian). (*After Luther.*) *H*, *Pinnotheres* (crustacean). (*After Koltzoff.*) *I*, *Homarus* (lobster). (*After Herrick.*) *J*, *Ascaris* (nematode): *a*, apical body; *n*, nucleus; *r*, "refractive body." (*After Scheben.*)

throughout the animal kingdom. Many minor variations in the behavior of these cell elements are known, however, and result in spermatozoa differing widely in general appearance (Fig. 150). In some groups no tail is present.

**The Structure of Other Ciliated Cells.**—In addition to gametes and zoöspores, there are other cells which possess special motor differentiations. Noteworthy in this connection are the ciliary mechanism of the ciliated epithelial cells of animals, and the flagellar apparatus of the Mastigophora. From the many situations which are known only a few illustrative cases will be selected.[1]

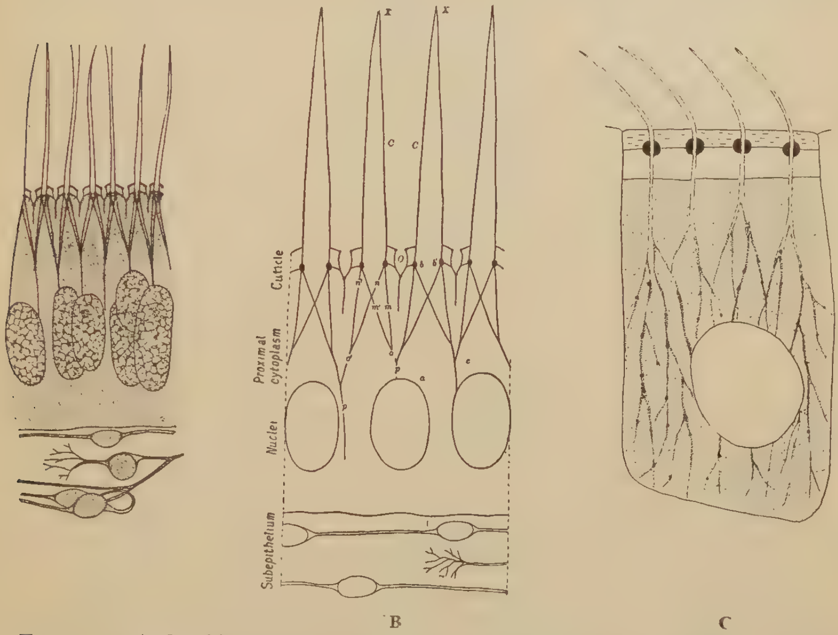

FIG. 151.—*A*, *B*, ciliary mechanism in *Lampsilis*. The cilia (*c*) are fused in pairs at their tips. Below the basal corpuscles (*b*) in the cuticle each cilium splits into two strands which connect with strands from other basal corpuscles. (*After Grave and Schmitt*, 1924.) *C*, diagram of a ciliated epithelial cell based on the figures of Saguchi (1917).

In ciliated epithelial cells each cilium is observed to be associated with a *basal granule* in or near the cell membrane. The nature of such basal granules has been the subject of a long controversy beginning with the statement of the theory that they, like the granules bearing the axial filament in the spermatozoön, are modified centrioles (Henneguy, 1897; Lenhossék, 1898). In an extensive review of the evidence Erhard (1911) concludes that it is on the whole unfavorable to the theory of centriolar derivation. This is also the opinion of Saguchi (1917), who has described as follows the insertion of the cilia in such cells (Fig. 151, *C*). At the base of each cilium, which itself shows no internal structural differentiation, there is always a basal corpuscle. The corpuscles, and hence the cilia, are in parallel rows; and beneath each row there is a transparent zone in which the rootlets of the cilia are anchored, and through which they pass and become continuous with strands of a cytoplasmic reticulum. Cilium, corpuscle, rootlet, and cytoplasmic strand form one continuous structure. Saguchi believes that neither the cilium nor the rootlet causes the ciliary movement, but that the kinetic center of this movement is in the basal corpuscles, as Henneguy and Lenhossék thought. Contrary to the opinion of these authors, however, he regards the ciliary apparatus as entirely independent of centrioles, holding rather that it is produced by the differentiation of chondriosomes, and that the resemblance of ciliated cells to spermatids, in which centrioles do produce the motor apparatus, is an accidental one.

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[1] For accounts of the flagellar apparatus of flagellates and Protozoa, see Minchin (1912), Hartmann (1911), and especially the papers by R. G. Sharp (1914), Yocum (1918), C. V. Taylor (1920), Rees (1921), McDonald (1922), Hall (1922), Kofoid and Swezy (1915–1923), Kofoid and Christiansen (1915). For discussions of cilia, see Heidenhain (1911) and Lundegårdh (1922), and the principal papers there cited.

The centriole theory is again favored by Helvestine (1921) and Jordan and Helvestine (1923). In the cells lining the efferent ducts of the epididymis of the white rat the rod-shaped corpuscles to which the cilia are attached appear to be centriole derivatives, and not genetically related to chondriosomes; but in other cells in the epididymis there are basal granules which seem rather to be cytoplasmic in nature.

Grave and Schmitt (1924, 1925) have made a further significant contribution to our knowledge of ciliated epithelial cells (Fig. 151, *A*, *B*). In gill cells of certain mollusks (*Lampsilis*, *Quadrula*) they find that the ciliary rootlets below the basal corpuscles are connected with one another and with the other parts of the cell in a very definite manner, forming a system which in all probability represents the structural basis for the coördinated action of the cilia. Such action has often been thought to be independent of any specially differentiated paths in the protoplasm.

That cilia may be withdrawn, and may show certain independent movements when amputated (Pütter, 1903; Pfeffer, 1904), together with the frequently described cilium-like behavior of pseudopodia, are facts of interest in connection with O. Hertwig's (1909) suggestion that cilia have been derived phylogenetically from pseudopodia of simple form.

Among the flagellates the flagellar or neuromotor apparatus, which is chiefly a derivative of the centrosome, may show an astonishing complexity. A comparatively simple type occurs in *Menoidium* (Hall, 1923) (Fig. 152, *E*). Here it consists essentially of a single flagellum, a blepharoplast, a centrosome at the surface of the nucleus, and a *rhizoplast* connecting the blepharoplast with the centrosome. At the time of cell-division the blepharoplast divides, its halves for some time remaining connected by a slender *paradesmose*. Kofoid and Swezy (1915*a*) further report that in *Trichomonas* each blepharoplast divides to form a new basal granule (blepharoplast proper) and a centrosome; hence the original blepharoplasts are called *centroblepharoplasts* (1919*a*). In *Giardia* the paradesmose connects the centrosomes rather than the blepharoplasts

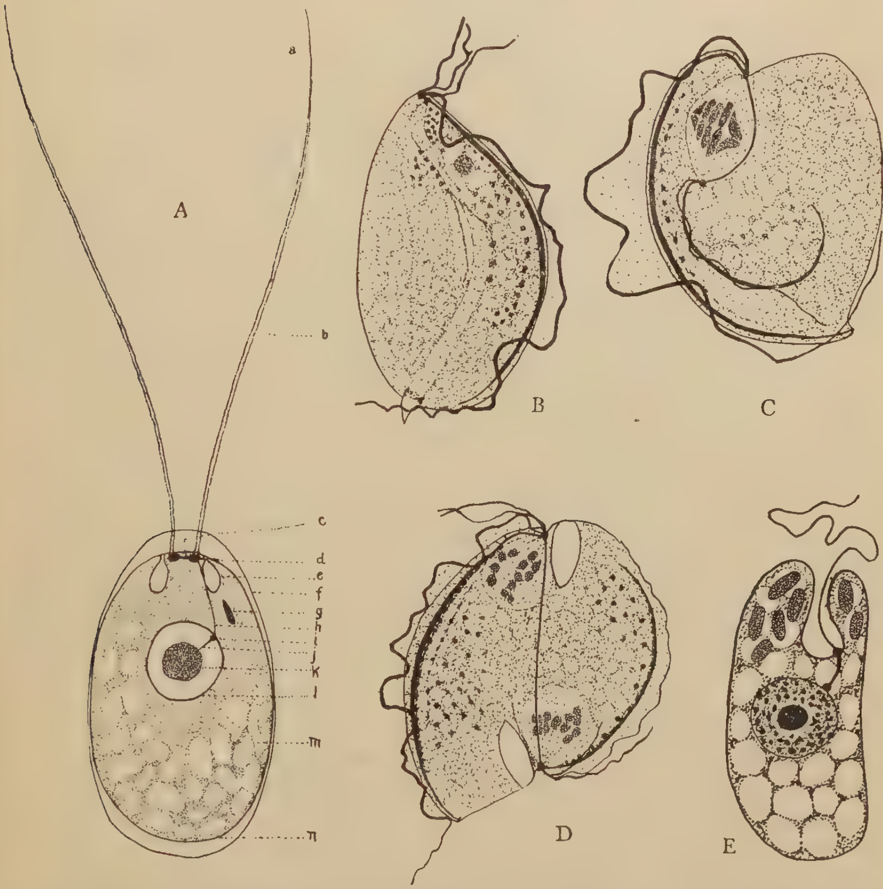

Fig. 152.—*A*, *Polytoma uvella:* *a*, end-piece of flagellum; *b*, uniform portion of flagellum; *c*, paradesmose, or lateronema; *d*, basal granule, or blepharoplast; *e*, contractile vacuole; *f*, cell envelope; *g*, eyespot; *h*, rhizoplast; *i*, centrosome, or anchoring granule; *j*, centronema; *k*, karyosome; *l*, nuclear membrane; *m*, starch; *n*, surface of protoplast. (*After Entz*, 1918.) *B*, *C*, *D*, *Trichomonas muris:* *B*, left side; *C*, metaphase of division; *D*, telophase with paradesmose still intact. (*After Wenrich*, 1921.) *E*, *Menoidium incurvum*, showing flagellum growing from blepharoplast, which is connected by a rhizoplast with a centrosome at the nuclear surface. In the upper part of the cell are paramylum bodies. (*After Hall*, 1923.)

(1922). In *Trichomonas muris* (Fig. 152, *B*, *C*, *D*) Wenrich (1921) finds no rhizoplast or centrosome at the nuclear surface, but only a blepharoplast which acts as a centrosome (centroblepharoplast). To this are attached a long flagellum forming the margin of the undulating membrane, and three shorter free ones. Along the base of the membrane and connected with the blepharoplast is a "chromatic basal rod," and within the cell may be seen certain other peculiar differentiations. As mitosis begins the blepharoplast buds off a smaller new one, and the two diverge like centrosomes to opposite poles of the achromatic figure, a paradesmose being drawn out between them. Apparently, one or two of the free flagella accompany the new blepharoplast, new ones later growing out to restore the full number. It is also accompanied by a new chromatic basal rod, which begins to differentiate as a row of granules even before the division of the original blepharoplast.

In *Polytoma uvella* (Fig. 152, *A*) the two flagella are inserted on two blepharoplasts which are connected with each other by a paradesmose and with the nucleus by a rhizoplast. The latter is in connection with the karyosome through an intranuclear granule and a filamentous *centronema*. It is stated that a chromatic body derived from the karyosome passes into the cytoplasm; there it divides to form a centriole, which is active in mitosis, and a second body which passes toward the cell surface, giving rise to the rhizoplast and a granule which divides to form the two blepharoplasts (Entz, 1918).

In the trypanosomes, as in the infusoria, there are two nuclei: the trophonucleus and the kinetonucleus. Motor mechanisms differ considerably within the group, but it seems that the flagellum is usually borne on a basal granule (centrosome?) associated with the kinetonucleus. At the time of cell-division the trophonucleus, kinetonucleus, and basal granule all divide. Although it was formerly thought that the flagellum also split, it now seems clear that it remains attached to one half of the divided basal granule, while a new one arises from the other half (Rosenbusch, 1909; Kuczynski, 1917; Hartmann and Nöller, 1918).

# CHAPTER XV

## SYNGAMY

It has already been pointed out that meiosis and syngamy constitute two exceedingly important crises in the life cycle. In meiosis the chromosomes of a diploid complement are assorted into haploid sets, which are then carried into the next generation through the spores and gametes. In *syngamy*, or the union of the gametes, there is not only an important physiological effect upon developmental processes, but also, in the union of the gamete nuclei, a combination of two such haploid chromosome sets to form a new diploid complement (*diplosis*). In the case of organisms having large female gametes and small, more active male gametes one ordinarily refers to syngamy as the *fertilization* of the egg by the sperm; but it should be borne in mind that the syngamic reaction is in all cases mutual, and that it is the fusion product of the two gametes which proceeds with development. As the finer details of syngamy and the significance of its results become better understood, the aptness of Huxley's (1878) often quoted simile, in which he compares the organism to "a web of which the warp is derived from the female and the woof from the male," becomes increasingly striking.

### PLANTS

Although the central act in the process of syngamy is regularly the union of two sexually differentiated nuclei, the morphological features associated with this fusion are exceedingly diversified in the different groups of plants. This is notably true of the algæ and fungi, in which the homologies of many of the phenomena observed are very uncertain.[1]

**Algæ.**—Fusions involving the various types of gametes described in the preceding chapter take place as follows. In *Ulothrix* the two motile isogametes meet and fuse to form a resting zygospore (Fig. 153, *A*). The exact manner of fusion varies greatly in such forms, but commonly it begins at the ciliated end. In *Ectocarpus* also the gametes are morphologically similar, but some of them become relatively passive and anchor themselves to the substratum by one cilium. The more active (male) gametes then attach themselves by one cilium to the anchored ones

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[1] For an extensive account of sexual and asexual cell and nuclear fusions in plants, see Tischler (1921–1922, Chap. 8). For the algæ, see Oltmanns (1922–1923). For fungi, see Guilliermond (1913*e*), Atkinson (1915), and Wager (1920).

(females) and gradually undergo fusion with them (Fig. 153, *B*). The fusion culminates in the union of the nuclei. In such gametic unions as those of *Ulothrix* and *Ectocarpus* the chromatophores undergo no fusion so far as known; in some cases they have been followed through unchanged into the new individual. In *Fucus* the large passive eggs, and the small motile spermatozoids are shed from the organs which bear them, their union occurring in the sea water. Many spermatozoids attach themselves to each egg by one cilium, but after one of them enters the egg the others move away. The male nucleus remains relatively small up to the time it fuses with the egg nucleus, and a centrosome with an aster appears near the nuclear membrane at the point where the male nucleus enters (Yamanouchi, 1909). This latter phenomenon, which is very suggestive of the fertilization process in animals, has also been observed in *Dictyota* (J. Williams, 1904).

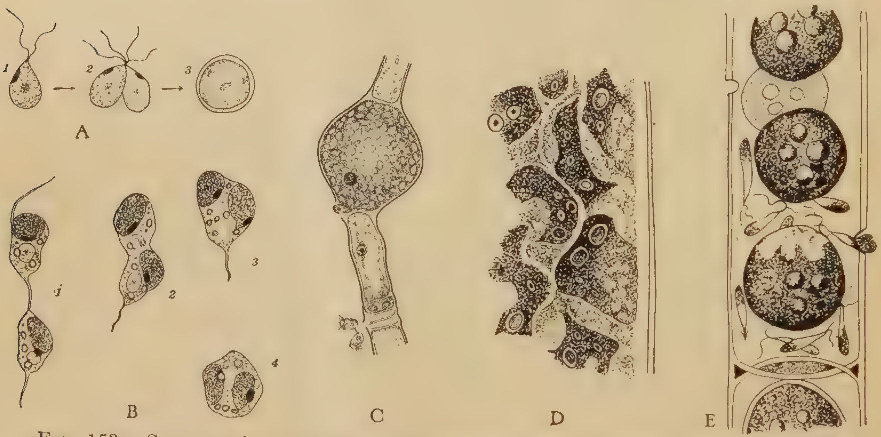

Fig. 153.—Syngamy in various algæ. *A*, gamete, union of similar gametes (isogamy), and zygote of *Ulothrix*. *B*, isogamy in *Ectocarpus siliculosus*. (*After Oltmanns*, 1897.) *C*, portion of filament of *Œdogonium;* spermatozoids escaping from antheridial cells below; spermatozoid about to enter egg above. (*After Coulter.*) *D*, the formation of eggs by subdivision of a cœnocytic protoplast in *Sphæroplea*. *E*, portion of filament of *Sphæroplea* showing several eggs; spermatozoids have entered through pores in filament wall. (*D* and *E after Klebahn.*)

In *Œdogonium* and *Vaucheria* the egg is not liberated from the oögonium, but is fertilized *in situ* by a spermatozoid, which passes into the oögonium through a specially differentiated pore and then enters the egg at a more or less distinct receptive spot. In the mature male gametes of *Vaucheria*, *Chara*, and *Coleochæte*, no plastids have been demonstrated, the new individual apparently deriving these organs wholly from the female gamete. Such statements, however, may require revision when male gametes have been more fully studied with methods specially devised for the investigation of cytoplasmic differentiations. In *Polysiphonia* the non-motile male gamete (spermatium) comes in contact with a prolongation (trichogyne) of the female sex organ (carpogonium). Solution of the intervening walls allows the nucleus of the spermatium to pass into the trichogyne and down to the female nucleus in the base of the carpogonium (Fig. 154, *A*). According to Yamanouchi (1906), the male nucleus, by the time it reaches the female nucleus, has resolved itself into a group of 20 chromosomes. In this condition it enters the female nucleus while the latter is yet in the reticular state. Soon the female reticulum becomes transformed into 20 chromosomes, which arrange themselves with the 20 paternal chromosomes in the spindle as the fusion nucleus divides. The spermatium of the Florideæ is said to carry no plastids.

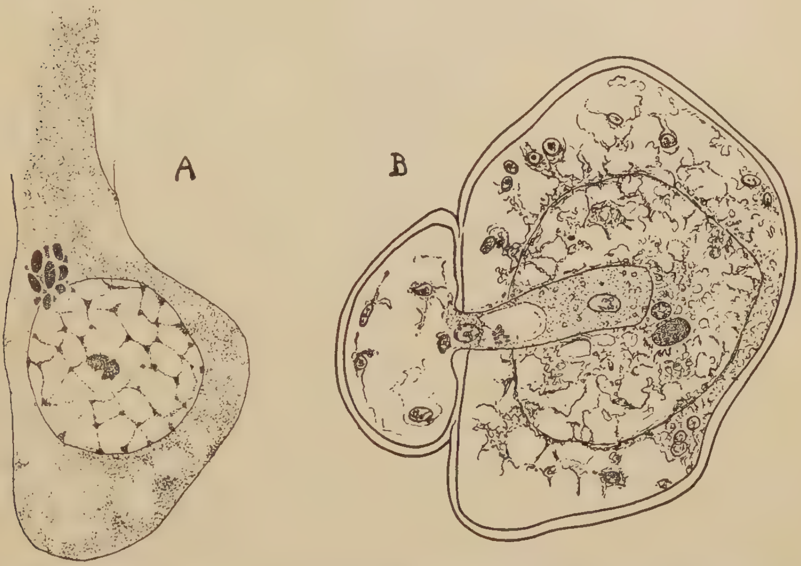

FIG. 154.—*A*, syngamy in *Polysiphonia*. Group of paternal chromosomes about to enter female nucleus. (*After Yamanouchi*, 1906.) *B*, syngamy in *Albugo candida:* female nucleus in center of oöplasm near the cœnocentrum (larger dark body); antheridial tube about to discharge a male nucleus. (*After Davis*, 1900.)

A special condition is found in the Conjugatæ (*Spirogyra*, *Zygnema*, *Mougeotia*, desmids, etc.). Here certain vegetative cells, with little morphological alteration, fuse in pairs to produce resting zygospores. In *Spirogyra*, for example, the entire protoplast passes through a conjugating tube to unite with a similar cell, commonly in another filament. The two nuclei fuse; but the plastids remain distinct, and those introduced by the contributing ("male") cell are observed in some species to degenerate in the zygospore (Fig. 104). In some species the zygospore is formed in the conjugating tube. The process of conjugation has recently been studied anew with great care by Lloyd (1925), who finds that it involves a remarkable activity on the part of contractile vacuoles.

In the diatoms a variety of precedures have been made known, especially through the researches of Karsten (1899–1912). The case of *Rhopalodia gibba*, as described by Klebahn (1896), will serve as an illustration. Two individuals meet and form a common mass of jelly between them. In each individual the nucleus undergoes two successive divisions, the protoplast then dividing into two portions, each with a large and a small nucleus. These two portions now fuse with the two produced by the other individual, forming two zygotes which develop into auxospores. In each case the large nuclei fuse and the small ones degenerate. In some diatoms the two uniting individuals show a distinct difference in sexual behavior.

**Fungi.**—Several types of sexual fusion are known among the oömycetes.[1] In *Albugo bliti* the egg has a large number of nuclei, and after the entrance of many male nuclei through the antheridial tube as many as 100 fusions may occur. In *Albugo candida, Peronospora parasitica,* and *Pythium* the uninucleate egg is entered by a single male nucleus (Figs. 129, 154, *B*). In *Saprolegnia* several uninucleate eggs are formed in the same oögonium, the antheridia sending in several tubes which deliver a male nucleus to each egg.

In the zygomycetes, represented chiefly by the Mucoraceæ, the extreme minuteness of the nuclei has made it impossible to follow their behavior with certainty. The contents of two multinucleate gametangia (*i.e.*, two cœnogametes) unite to form a zygospore. It is generally thought that, although some of the nuclei may degenerate, many fusions nevertheless occur,[2] but the claim has also been made that there is only one fusion (Macormick on *Rhizopus nigricans*, 1912). Baird (1924) observes no fusions.

In the ascomycetes the fusion of two nuclei in the ascus was first described by P. A. Dangeard (1894), who regarded it as a sexual act (Fig. 155, *A*). The matter soon became complicated when a number of cytologists, beginning with Harper (1895, etc.), found what appeared to be a nuclear fusion at an earlier stage in the life cycle. This fusion was reported to occur in the archicarp after the entrance of the contents of an antheridium,[3] in the archicarp when the antheridium is functionless or absent,[4] or in the vegetative cells when the archicarp is functionless or absent.[1] This early fusion came to be regarded as the sexual one, that in the ascus accordingly being looked upon as vegetative in nature. Some workers described a "double reduction" in the ascus to compensate for the two nuclear fusions (see p. 244).

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[1] Trow (1895–1904), Wager (1896, 1900*b*), Stevens (1899, 1901), B. M. Davis (1900, 1903, 1905), Miyake (1901), Claussen (1908).

[2] P. A. Dangeard (1906), Moreau (1911, 1913, 1915), Keene (1914), Burgeff (1915).

[3] Harper (1895–1905) on *Sphærotheca, Erisiphe, Pyronema,* and *Phyllactinia;* Blackman and Fraser (1905) on *Sphærotheca;* Claussen (1905) on *Boudiera.*

[4] Blackman and Fraser (1906) on *Humaria granulata;* Fraser (1907) on *Lachnea stercorea;* Welsford (1907) on *Ascobolus;* Dale (1909) on *Aspergillus.*

In a series of somewhat later researches another group of observers found the evidence for an early fusion to be very unsatisfactory. It appeared that, although nuclei become associated in pairs at an early stage and divide conjugately throughout the development of the ascogenous hyphæ, there is no fusion of nuclei until the ascus is formed. Furthermore, these observers could discover no "double reduction." They consequently concluded that the only nuclear fusion in the life cycle is that in the ascus, which is therefore to be regarded as a sexual act, as Dangeard held.[2]

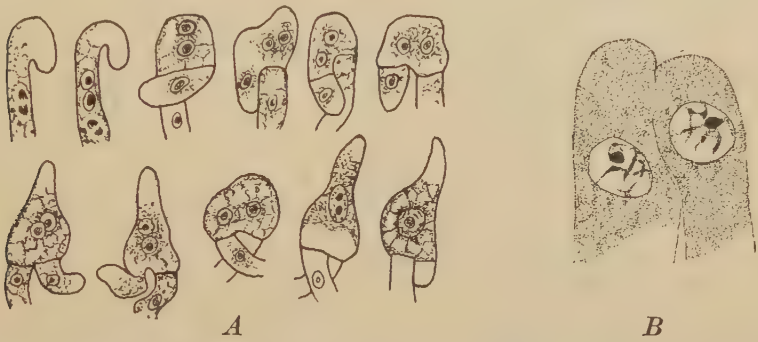

FIG. 155.—*A*, nuclear fusion in ascus of *Peziza vesiculosa*. (*After Dangeard*, 1894.) *B*, fusion of tips of hyphæ in æciospore sorus of *Phragmidium speciosum*. (*After Christman*, 1905.)

As the two nuclei fuse in the young ascus Harper (1905) observed in the case of *Phyllactinia corylea* not only a union of the chromatic systems, but also of the nucleoli and centrosomes, upon which the chromatic strands converge. In the ascomycetes generally the fusion nucleus, or "primary ascus nucleus," initiates three successive mitoses to form the eight ascospore nuclei. In certain yeasts it has been shown that the production of ascospores is preceded by a union of two cells with a fusion of their nuclei, the fusion nucleus dividing to form the spore nuclei (see Guilliermond, 1920).

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[1] Fraser (1907, 1908) on *Humaria rutilans;* Carruthers (1911) on *Helvella;* Blackman and Welsford (1912) on *Polystigma.*

[2] Among the researches supporting this view may be cited those of Claussen (1907, 1912) on *Pyronema;* W. H. Brown (1909, 1910, 1911*b*) on *Pyronema, Leotia,* and *Lachnea;* Faull (1911, 1912) on *Laboulbenia;* Nienburg (1914) on *Polystigma;* Ramlow (1914) on *Ascophanus* and *Ascobolus;* F. Brooks (1910) on *Gnomonia;* McCubbin (1910) on *Helvella;* H. B. Brown (1913) on *Xylaria;* Fitzpatrick (1918*a*) on *Rhizina;* Frey (1924) on *Venturia;* and S. G. Jones (1925) on *Rhytisma.*

Among the basidiomycetes the nuclear cycle first became known in the Uredineæ (rusts), owing to the researches of Blackman (1904), Christman (1905), and a number of later writers. In the typical rust life cycle there is a fusion of uninucleate cells at the base of the æcial sorus (Fig. 155, *B*). The binucleate cells thus arising produce the binucleate æciospores; and these upon germination form a mycelium with binucleate cells, the two nuclei dividing in unison ("conjugately") before each cell-division. After producing a series of crops of binucleate uredospores, this mycelium eventually bears teliospores which may consist of one or more cells. In each cell of the teliospore the two nuclei delivered to it as the result of the conjugate divisions throughout the binucleate mycelium finally unite, initiating the uninucleate phase of the life cycle. Here the fusion of cells and the fusion of their nuclei—two events which in most organisms occur in rapid succession—are widely separated in the cycle. It is questionable how far the cell fusion should be regarded as sexual; it is probably best regarded as a case of pseudomixis, or pseudogamy (Kurssanow, 1915) (see next chapter).

In the hymenomycetes it has long been known that a fusion of two nuclei occurs in the basidium, itself the terminal cell of a hypha with binucleate cells, prior to the formation of the four basidiospore nuclei (Fig. 105). Only more recently, however, has light been thrown upon the origin of the binucleate condition.[1] In certain species of several genera, including *Coprinus*, *Aleurodiscus*, *Panæolus*, and *Schizophyllum*, it has been shown that the plants are heterothallic, and that carpophores, although they will sometimes develop on a mycelium from a single spore, appear freely only when mycelia from different spores are intermingled. Unions then occur between hyphæ of different sexual strains, with the resulting formation of binucleate mycelia. The paired nuclei divide conjugately before each cell-division, their descendants eventually fusing in the basidium. It is further known that a segregation of sex factors occurs in the meiotic divisions of the fusion nucleus, so that the spores of a quartet produce mycelia differing in sexual reaction (p. 426). This is essentially similar to the situation in heterothallic phycomycetes. In the heterothallic *Panæolus campanulatus* the basidia of carpophores occasionally developed "apogamously" by a unisexual mycelium are known to be uninucleate; there is neither nuclear fusion nor meiosis, and the spores are all of one sex (Vandendries). In two species (*Coprinus radians:* Vandendries; *Schizophyllum commune:* Kniep) it has been observed that an ordinarily unisexual mycelium may later show an anastomosis of its branches, an early heterothallic phase thus giving way to a homothallic phase. Whether or not any species is rigidly heterothallic or completely homothallic is consequently a debated question.

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[1] Kniep (1915–1923), Bensaude (1918), Lehfeldt (1922), Vandendries (1923*ab*, 1924, 1925*ab*), Mounce (1921, 1922), Hanna (1925).

**Bryophytes and Pteridophytes.**—Although the grosser features of syngamy in bryophytes and pteridophytes have frequently been described, the details of the process have been worked out in very few cases. In certain bryophytes[1] the spermatozoid is transformed into a reticulate nucleus as it passes from the point of entrance into the egg toward the female nucleus (Fig. 156). The fate of the non-motile elements of the spermatozoid (cytoplasm, blepharoplast, and cilia) is unknown, but they seem to be absorbed by the egg cytoplasm. In *Sphærocarpos* it seems likely that the two sexual nuclei as such undergo no fusion, but give rise separately to their chromosomes which then take their places in a common cleavage spindle, as in a number of animals. Contrasted with this is the condition observed by Showalter (1926) in *Riccardia* (Fig. 158).[2] Here the elongated body of the spermatozoid applies itself to the surface of the egg, becomes more slender, and gradually sinks through the membrane into the cytoplasm. The chromatic matter of the egg nucleus contracts, and one end of the sperm extends through the nuclear membrane, where it becomes considerably swollen. The female nuclear matter then loosens up, and the swollen end of the penetrating

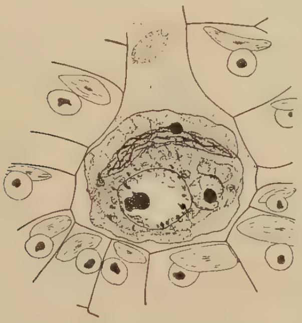

Fig. 156.—Syngamy in *Anthoceros*. Male and female nuclei about to fuse in lower part of egg in venter of archegonium; elongated plastid above them. Gametophyte cells show one nucleus and one plastid each.

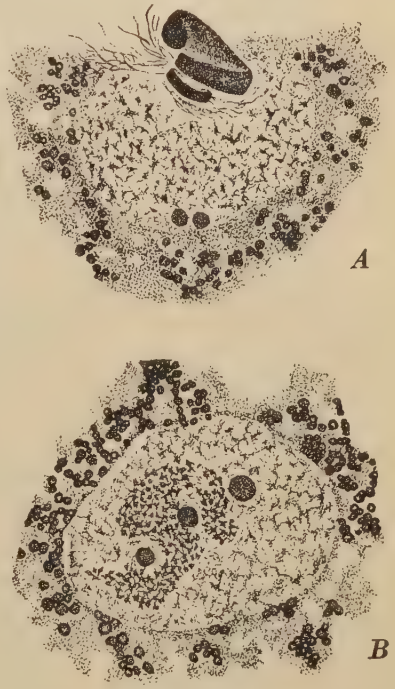

Fig. 157.—Syngamy in *Nephrodium*. The spermatozoid passes directly into the egg nucleus and there forms a reticulum. (*After Yamanouchi*, 1908.)

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[1] *Riccia* (Garber, 1904; Black, 1913); *Corsinia* (K. Meyer, 1911); *Preissia* (Graham, 1918); *Reboulia* (Woodburn, 1920); *Sphærocarpos* (Rickett, 1923); *Fissidens* (Gayet, 1897).

[2] The author is indebted to Dr. Showalter for allowing him to copy his drawings in advance of their publication elsewhere.

sperm is seen to lose its definite outline and differentiate a chromatic reticulum and a nucleolus. After penetration is complete the female and male reticula remain distinguishable for some time, but in the late prophase and the metaphase of the first embryonal mitosis the chromosomes of the two parents form a single group.

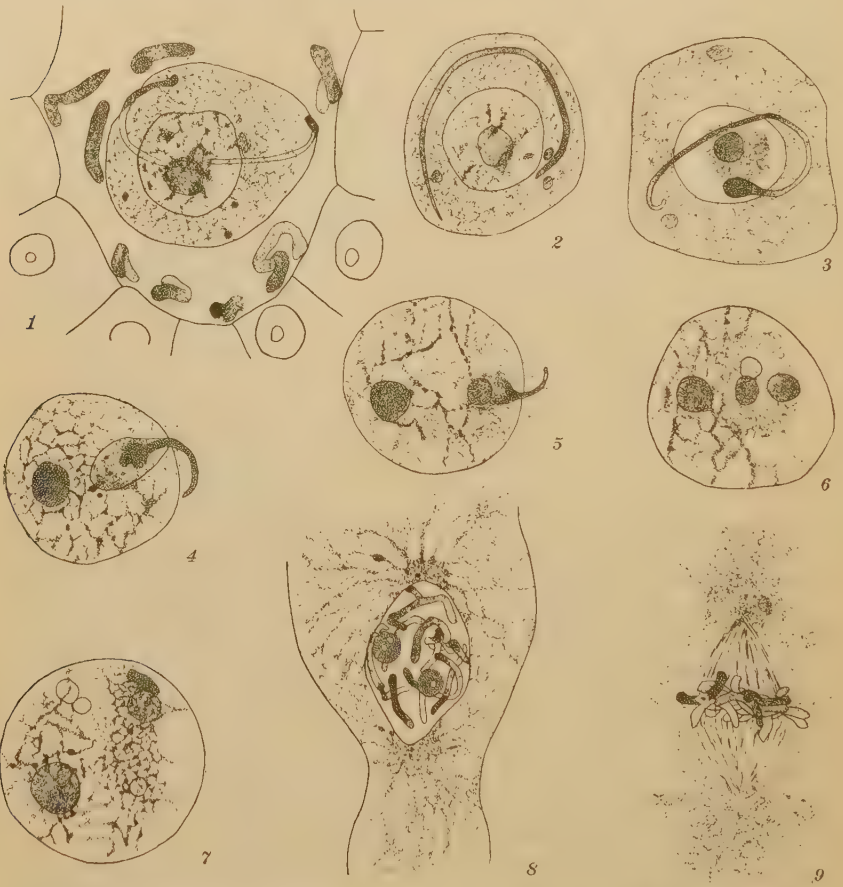

FIG. 158.—Syngamy in *Riccardia*. 1, several spermatozoids near egg in archegonium; one spermatozoid lying against egg. 2, spermatozoid in egg cytoplasm. 3–7, passage of spermatozoid into egg nucleus, and its transformation into a reticulum distinguishable from that of the egg nucleus. 8, 9, first mitosis in zygote; paternal and maternal chromosomes intermingled. (*After Showalter*, 1926.)

In *Preissia* Graham (1918) has described two centrosomes with weakly developed asters in the cytoplasm of the egg at the time when the two sexual nuclei are approaching each other and in contact (Fig. 68). This, together with the observations of Yamanouchi on *Fucus* and of Williams on *Dictyota* (p. 322), suggests that in certain plants, as in animals, the differentiation of division centers in the egg cytoplasm is in some way induced by the entrance of the spermatozoid. The fate of the non-nuclear portions of the spermatozoid may prove to be of interest in this connection.

Syngamy in pteridophytes has been described in detail for *Onoclea* (Shaw, 1898*b*) and *Nephrodium* (Yamanouchi, 1908). In both cases the multiciliate spermatozoid enters bodily into the egg nucleus with no previous alteration into the reticular state. Here it gradually becomes reticulate and irregular in shape, until finally its limits are indistinguishable, the chromatic material contributed by the two gametes apparently forming a single fine-meshed network (Fig. 157). This seems to be a general condition in ferns. In *Pilularia*, however, Campbell (1888) reported that the male nucleus becomes considerably transformed before the fusion.

In bryophytes and pteridophytes, so far as known, the spermatozoid brings no plastids into the egg. Plastids may frequently be seen through oögenesis and in the egg (Fig. 156), but they seem to disappear during spermatogenesis. Further studies on the male cytoplasm with new methods might yield interesting information on this point.

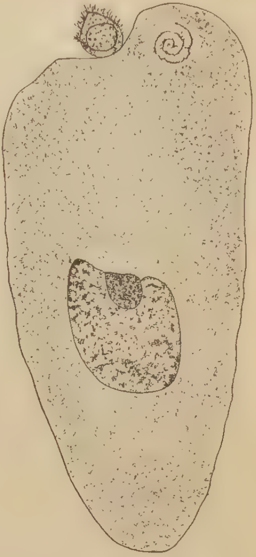

Fig. 159.—Syngamy in *Zamia*. Male and female nuclei uniting at center; cytoplasmic sheath and spiral blepharoplast of spermatozoid above; another spermatozoid at surface of egg. (*After Webber*, 1901.)

**Gymnosperms.**—In the cycads and *Ginkgo*, which have motile spermatozoids, syngamy occurs as follows:[1] The pollen tube discharges two spermatozoids into the archegonial chamber, and one of them squeezes between the neck cells of the archegonium into the egg. The nucleus of the spermatozoid then frees itself from the cytoplasmic sheath with its blepharoplast and cilia, and advances alone to the egg nucleus, with which it fuses (Fig. 159). The structures left behind are absorbed in the cytoplasm.

In the Coniferales and Gnetales the male cells have no motile apparatus. Each consists of a nucleus surrounded by a more or less sharply delimited mass of cytoplasm. In most cases this cytoplasm remains intact until after the male cell has entered the egg, but in other forms, such as *Pinus*, it mingles with the cytoplasm of the pollen tube, so that only male nuclei, rather than completely organized male cells, are delivered to the egg. All the nuclei present in the pollen tube—stalk nucleus, tube nucleus, the two male nuclei, and, in certain species, free prothallial nuclei—may be discharged into the egg. All but the functioning male nucleus usually degenerate at once, but in some cases they have been observed to undergo division.

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[1] Hirasé (1895, 1918) and Ikeno (1901) on *Ginkgo;* Ikeno (1898) on *Cycas;* Webber (1901) on *Zamia;* Chamberlain (1910, 1912, 1916) on *Dioön*, *Ceratozamia*, and *Stangeria*.

When a complete male cell enters the egg the cytoplasm of the former shows two general modes of behavior. In some species it may be left behind in the peripheral region of the egg as the male nucleus frees itself and advances alone to the female nucleus.[1] In *Sequoia* (Lawson, 1904) the male nuclei escape from their cytoplasm before their discharge from the pollen tube, and enter the egg alone. In another group of species the male cytoplasm remains intact and invests the fusing sexual nuclei, being clearly distinguishable from the cytoplasm of the egg. The pollen tube cytoplasm often plays a conspicuous part in the formation of this "mantle." The significance of this phenomenon can only be conjectured.[2]

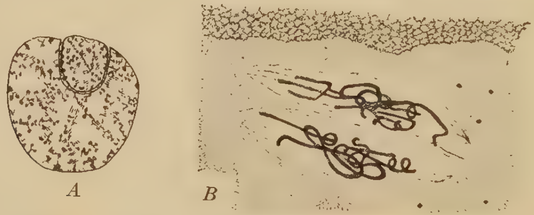

Fig. 160.—Syngamy in *Pinus*. *A*, male nucleus pressing into female nucleus; *B*, first embryonal mitosis, showing separate paternal and maternal chromosome groups. (*After Ferguson*, 1904.)

The behavior of the chromosomes during the fusion of the gametic nuclei and the first embryonal division has been described in a number of conifers; similar data for the cycads are as yet comparatively few. As a general rule the chromatic elements of the two nuclei, although in the reticular condition when the nuclei unite, do not become very intimately associated in the fusion nucleus, but remain distinguishable until the first embryonal mitosis occurs. They then develop two groups of chromosomes which become arranged in a common achromatic figure (Fig. 160). Such an independent formation of the paternal and maternal chromosome groups has been observed in several conifers.[3] In *Sequoia*, on the contrary, Lawson (1904) reports that the two nuclei form a common reticulum in which the parental contributions cannot be distinguished. With regard to the first embryonal mitosis, the general opinion is that all the chromosomes, paternal and maternal, split longitudinally, the daughter chromosomes being distributed to the daughter nuclei as in any other somatic mitosis. This type of behavior was described for the chromosomes of *Pinus* by Ferguson (1904) and soon came to be regarded as general for conifers, as it had been for other organisms.

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[1] This has been reported in *Pinus* (Ferguson, 1901, 1904), *Thuja* (Land, 1902), *Juniperus* (Norén, 1904), *Cryptomeria* (Lawson, 1904), *Libocedrus* (Lawson, 1907), and *Ephedra* (Berridge and Sanday, 1907).

[2] It has been observed in *Taxodium* (Coker, 1903), *Torreya* (Robertson, 1904; Coulter and Land, 1905), *Cephalotaxus* (Coker, 1907), *Phyllocladus* (Kildahl, 1908), *Juniperus* (Nichols, 1910), *Agathis* (Eames, 1913), and *Taxus* (Dupler, 1917).

[3] *Pinus* (Blackman, 1898; Chamberlain, 1899; Ferguson, 1901, 1904); *Larix* (Woycicki, 1899); *Tsuga* (Murrill, 1900); *Juniperus* (Norén, 1907); *Cunninghamia* (Miyake, 1910); *Abies* (Hutchinson, 1915).

A somewhat different mode of chromosome behavior has been reported in *Abies* by Hutchinson (1915) and in *Stangeria* by Chamberlain (1916). Here the double chromosomes in the first embryonal division appear in the haploid number, which seems to indicate a pairing rather than a longitudinal splitting. In the anaphase the diploid number passes to each pole. What has occurred in the meantime is uncertain, but Hutchinson believes the paired chromosomes become doubled through a transverse segmentation. Because of the theoretical significance attached to the transverse segmentation of chromosomes and to their separation without splitting (disjunction), the above interpretation calls for the most critical verification.

**Angiosperms.**—The pollen tube, which is the elongated tube-cell bounded by the greatly extended intine, grows from the stigma through the style to the ovarian cavity, and then by way of the micropyle of the ovule through the nucellus and into the embryo sac (Fig. 107). Usually the tube makes its way between the cells of the style by means of enzymes which dissolve the middle lamellæ of their walls (Paton, 1921). After entering the sac the tube ruptures at its end, dicharging the two male gametes, together with a certain amount of pollen tube cytoplasm and sometimes the tube nucleus. Frequently the tube appears to pass directly through a synergid. It has already been pointed out (p. 304) that the male gametes may be complete cells or only nuclei with no specially delimited cytoplasm. Frequently the nuclei are markedly vermiform. *Double fertilization*, a process peculiar to angiosperms, now takes place: one of the male nuclei enters the egg and fuses with its nucleus, thus forming the primary nucleus of the embryo, while the other male nucleus fuses with the two polar nuclei to form the primary endosperm nucleus (Figs. 107, 161).

*The Gametic Fusion.*—So far as observations enable one to say, only a male nucleus is definitely known to enter the egg. In nearly all descriptions it is stated that, although distinct male cells may be present in the pollen tube, their cytoplasm later mingles with that of the tube or embryo sac, leaving the male nuclei free to pass alone to the egg and polar nuclei.[1] In *Vallisneria*, on the contrary, Wylie (1922, 1923) shows that the male cytoplasm remains distinct until the surface of the egg is reached. The same appears to be true of *Asclepias cornuti* also (Finn, 1925). How far equally careful examination would show this to hold for other cases is uncertain. Although the male cytoplasm may sometimes be traced to the egg membrane, none has yet been definitely seen to enter the egg along with the male nucleus. It would obviously be a matter of extreme difficulty, however, to demonstrate conclusively that in passing through the egg membrane the nucleus is absolutely freed of all adhering cytoplasm, chondriosomes, or plastid primordia; such a demonstration has not yet been given in any case. Wylie considers it possible that some or possibly all of the cytoplasm of the male cell enters the egg of *Vallisneria*. It is scarcely necessary to point out the bearing of this point on problems relating to the inheritance of characters manifesting themselves in cytoplasmic bodies, such as plastids (see p. 417).

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[1] *E.g.*, S. Nawaschin (1910) and Welsford (1914) on *Lilium*. Many reported cases of the entrance of a naked nucleus into the egg are listed by Tischler (1921–1922, p. 486).

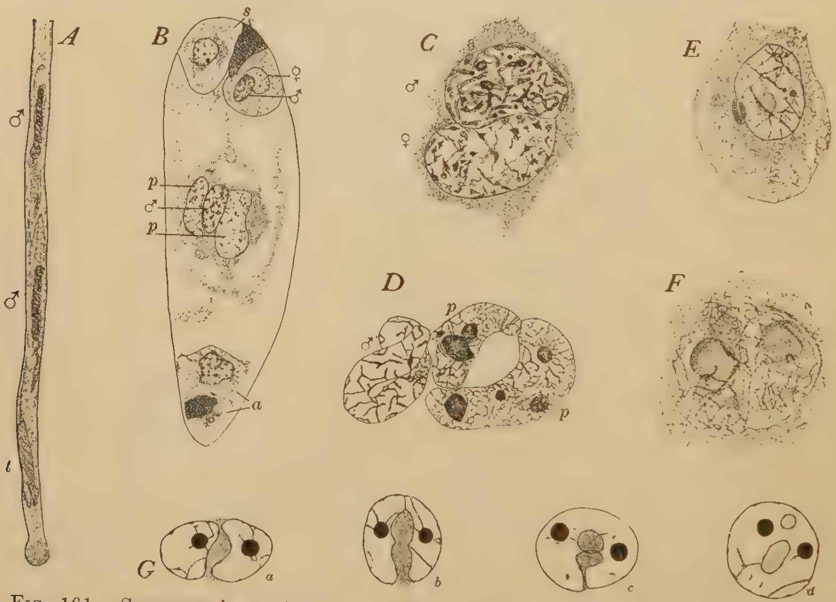

Fig. 161.—Syngamy in angiosperms. *A*, end of pollen tube from basal portion of style of *Lilium auratum*, showing two male cells and tube nucleus. (*After Welsford*, 1914.) *B*, double fertilization in *Lilium canadense:* sexual nuclei about to fuse in egg; second male and two polar nuclei fusing at center of embryo sac; *s*, synergids, one degenerated; *a*, antipodal cells. *C*, fusion of sexual nuclei in egg of *Lilium philadelphicum*. (*After Weniger*, 1918.) *D*, the second male and two polar nuclei in *Lilium Martagon*. (*After Nothnagel*, 1918). *E*, vermiform male nucleus in contact with egg nucleus in *Triticum durum*. (*After Sax*, 1918.) *F*, spireme stage of triple fusion nucleus in *Triticum durum*, showing distinctness of chromatic elements of the three nuclei. (*After Sax*.) *G*, inclusion of cytoplasm in fusing sexual nuclei of *Peperomia sintenesii;* this seems to be an occasional phenomenon with no special significance. (*After W. H. Brown*, 1918*b*.)

The fusion of the two sexual nuclei probably occurs in most cases very soon after they come in contact, though in certain forms it is known to be considerably delayed. The karyotin of the two nuclei at the time these unite may be in the reticular condition, the male and female elements being indistinguishable in the fusion nucleus. This situation was described by most of the earlier workers,[1] and has also been more recently reported by Sax (1916) in his work on *Fritillaria.* In other cases, as was early shown by Guignard (1891), the karyotin has already reached the spireme stage characteristic of the prophase, the paternal and maternal elements being distinguishable in the spindle in the ensuing division of the zygote. Such is the condition, for instance, in *Calopogon* (Pace, 1909), *Trillium* (Nothnagel, 1918), and *Lilium* (Weniger, 1918). That the same species may show considerable variation in this respect is indicated by the situation in *Fritillaria,* in which Sax (1916, 1918) finds that fusion, though it usually occurs in the reticular stage, sometimes takes place after the spiremes have been developed. Weniger (1918) reports that in *Lilium philadelphicum* and *L. longiflorum* the egg nucleus is in the reticulate condition and the male nucleus in the spireme stage at the time of union.

With regard to the behavior of the two gametic sets of chromosomes, it has been generally held that, whatever their condition at the time of the nuclear union, all of them, both paternal and maternal, split longitudinally at the first division of the zygote, the daughter chromosomes so formed being distributed to the two resulting nuclei, just as in all the subsequent somatic divisions. Recently, however, Weniger (1918) has reported a condition in *Lilium* similar to that described by Hutchinson (1915) for *Abies:* the maternal and paternal chromosomes form pairs and divide transversely into daughter segments which pass to the poles. With this conclusion other recent investigations of syngamy in angiosperms are not in agreement. Nothnagel (1918) finds in *Trillium* no such pairing and cross segmentation, and states that each chromosome splits longitudinally as held by Ferguson for *Pinus* and by cytologists in general. Sax (1918) also shows that each paternal and maternal chromosome in *Fritillaria* and *Triticum* divides longitudinally, the first embryonal division involving no disjunction of whole chromosomes or chromosome segments.

*In syngamy two haploid sets of chromosomes are brought together and form a new diploid complement; and since every chromosome of this complement divides equationally at every somatic mitosis throughout the development of the resulting individual, every nucleus in this individual contains a descendant of every chromosome originally present in the zygote.* The cardinal importance of these facts in connection with current theories of heredity will be apparent in subsequent chapters.

*The Endosperm Fusion.*—The fusion of the second male nucleus with the two polar nuclei of the embryo sac to form the primary endosperm nucleus may be carried out in a variety of ways. The most commonly reported mode is that in which the two polars unite to form a *polar fusion nucleus* ("embryo sac nucleus") before the entrance of the pollen tube, the male nucleus later being added. Ernst (1902), for example, found this to be the method in *Paris quadrifolia.* Less frequently the male nucleus meets and fuses with the polar nucleus of the micropylar end of the sac, the other polar then fusing with the product. This is the method described by S. Nawaschin (1898, 1899) in his account of the discovery of double fertilization in *Lilium Martagon* and *Fritillaria tenella.* The simultaneous fusion of all three nuclei appears to be a common occurrence; it has recently been described in some detail by Nothnagel (1918) for *Trillium* and *Lilium.* Just as in the union of the first male nucleus with the egg nucleus, the karyotin of the second male and two polar nuclei may be in either the reticular or the spireme condition as they come together. In *Lilium Martagon* (Nothnagel) it is in the form of fine strands, intermediate between the resting and spireme stages (Fig. 161, *D*). Although the three nuclei often appear exactly alike, it is frequently possible to distinguish the male from the polars, not only by its shape and smaller size, but by the condition of its karyotin. In *Lilium longiflorum* (Weniger, 1918), for example, the male nucleus is in the spireme stage while the polar nuclei are still in the reticular condition. The membranes of the three nuclei may persist for some time after they come into intimate contact, and even after they have disappeared the chromatic elements of the three constituent nuclei may in many cases be distinguished if the section has been made in a favorable plane. When fusion occurs in the metabolic stage this is not so apparent, but when it occurs in the spireme stage the three chromatic groups are made out with little difficulty.

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[1] *E.g.,* Strasburger (1900*b*, 1901*b*), S. Nawaschin (1898, 1899), Ernst (1902), and Mottier (1904*b*).

As the division of the endosperm nucleus approaches, the spiremes of its three constituent nuclei become increasingly distinct, even if one or more of the nuclei have fused in the reticular condition. Nothnagel, Weniger, and Sax in their recent studies all report this condition (Fig. 161, *F*). As the spiremes are developed into fully formed chromosomes all of them (the triploid number) split longitudinally, no observer reporting such a pairing as some have thought to occur between the chromosomes of the egg and first male nuclei. Nothnagel describes the formation of a tripolar spindle about the chromosomes; the bipolar condition soon develops from this. How frequently this may occur is not known. In any case the mitosis then proceeds along the usual lines and each of the two daughter nuclei receives the triploid number of chromosomes. This number characterizes all of the subsequently formed endosperm nuclei.

Although endosperm is formed by the repeated division of a triple fusion nucleus in the great majority of known examples, cases are known in which it is produced by the polar fusion nucleus alone without the male, or by the fusion product of the male and one polar, or by one polar alone. Combinations of these three methods may be found in the same embryo sac. The development of the endosperm may be initiated by the formation of a number of free nuclei which later become separated by walls, or by the formation of walled cells from the start.[1]

## ANIMALS

The story of syngamy in many animals[2] is complicated by the fact that both the maturation of the egg and its fertilization may proceed simultaneously. In echinoderms and some other forms maturation is completed before the spermatozoön penetrates. In certain other animals it proceeds as far as the metaphase of the first meiotic mitosis (*Chætopterus*, *Cerebratulus*) or the prophase of the second mitosis (many vertebrates), but does not go further unless penetration occurs. Finally, in the marine annelid, *Nereis*, the germinal vesicle undergoes no change unless the spermatozoön has entered the egg. In spite of such complications, however, the large free eggs of certain animals, notably those of echinoderms, afford experimental material far superior to anything known among plants, and have played a large part in the development of our knowledge of syngamy and other cytological phenomena.

*The Entrance of the Spermatozoön into the Egg.*—Probably in most animals the whole spermatozoön enters the egg (Fig. 162). In some sea urchins only the head and middle piece enter, while in *Nereis* the head alone passes in, leaving the middle piece and tail on the egg surface. The details of penetration in two of the best-known cases are as follows.

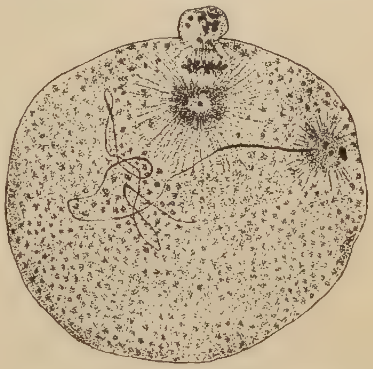

FIG. 162.—Syngamy in *Physa* (snail). Sperm head and amphiaster at right, with long flagellum extending toward left; second meiotic division in progress. (*After Kostanecki and Wierzyski*, 1896.)

In *Nereis* (F. R. Lillie, 1912, 1919) the egg has a tough vitelline membrane, an alveolar cortical layer, many yolk and oil droplets, and a large central germinal vesicle (nucleus). If many spermatozoa are present in the vicinity, a large number attach themselves to the egg, but usually all but one are carried away by an outflow of jelly from the alveoles of the cortical layer. This layer now takes the form of a zone traversed by radial protoplasmic plates representing the walls of the alveoles. A transparent "fertilization cone" extends from the inner region of the egg across this zone and touches the membrane at the point where the spermatozoön is beginning to penetrate. The perforatorium goes through the egg membrane and becomes attached to the transparent cone. The latter is now withdrawn, carrying the head of the spermatozoön into the egg with it. Thus it appears that the initiative for the final act of penetration lies with the egg rather than with the spermatozoön. Since only the head enters the egg in *Nereis,* it seems clear that the only necessary portion of the spermatozoön in the actual union is the nucleus; the middle piece and tail are accessory and function only as locomotor organs.

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[1] See Coulter and Chamberlain (1903), Samuelsson (1913), Jacobson-Stiasny (1914), Dahlgren (1922, 1923), Stenar (1925), and Svensson (1925).

[2] In the preparation of this portion of the chapter the author has drawn very freely upon Professor F. R. Lillie's *Problems of Fertilization*, (1919). See also Lillie and Just (1924), Doncaster (1920), Agar (1920), and Wilson (1925).

In the starfish (Chambers, 1922*c*, 1923*b*) (Fig. 163) the blunt-headed spermatozoa swim about with spasmodic movements, and apparently by chance come in contact with the thick zone of sticky jelly surrounding the egg. The egg then responds to the presence of the entangled spermatozoa by forming one or more hyaline conical projections on its surface. From the summit of each cone a delicate filament grows outward through the jelly until it touches and adheres to any sperm head (now motionless) which happens to lie in its path. The filament then retracts, drawing the spermatozoön inward through the jelly to the summit of the cone. Other filaments are at the same time withdrawn whether they have secured spermatozoa or not. When the spermatozoön arrives at the surface of the cone it is immediately engulfed and passes deeper into the egg. The cytoplasmic granules at the base of the cone disappear, leaving a hyaline pathway along which the sperm head glides. Other spermatozoa being drawn through the jelly are usually dropped by the

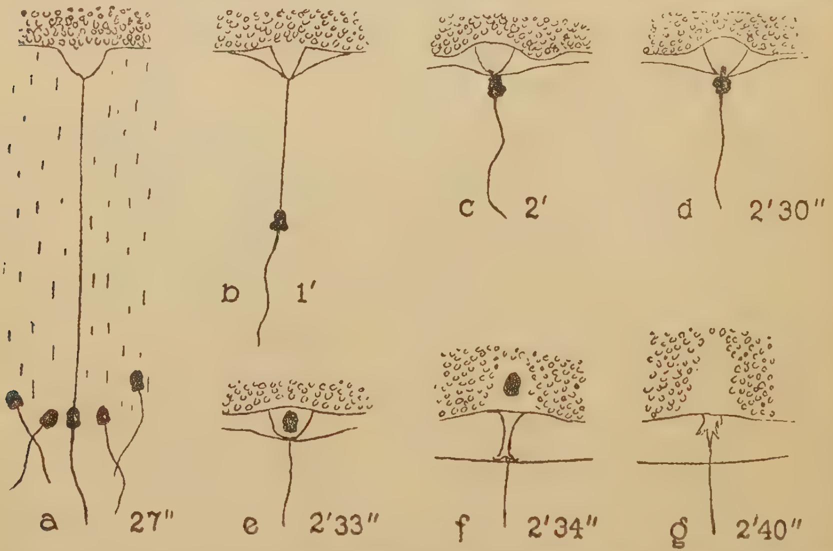

Fig. 163.—The entrance of the spermatozoön into the egg of the starfish. The time occupied by the process is indicated. (*After Chambers*, 1923*b*.)

retracting filaments when the first sperm enters the egg; in case they do reach the egg surface they are stopped by the newly formed fertilization membrane.

The most striking feature in both of these cases is the relatively passive rôle played by the spermatozoön. Instead of actively forcing its way into the egg by its own power, as many have been accustomed to think, it is "swallowed" by the egg after its own movements have ceased. In this connection Bowen (1923, 1924*ab*) has advanced the view that the acrosome with its perforatorium is not a cutting tool, but "essentially a secretory product the principal function of which is to initiate the physico-chemical reactions of fertilization." The spermatozoön may show no such movements as would be necessary for the use of a cutting or boring tool, and in some animals the acrosome is neither of the right shape nor properly located to act in such a capacity.

The immediate visible effects of the entrance of the sperm are seen chiefly in changes in the appearance of the cortical region of the egg. If a vitelline membrane is present, as in vertebrates, a "perivitelline space" usually appears between the membrane and the egg; and this space may in some cases (frog) be great enough to permit the rotation of the egg within the membrane. A *fertilization membrane* is commonly formed as a result of fertilization. In the echinoderm it first appears at the point where the spermatozoön is attached and spreads over the egg with great rapidity; this really consists in the elevation of a delicate membrane already present, a process which Heilbrunn (1924*c*) has associated with a lowering of surface tension. These cortical changes do not depend upon the actual entrance of the spermatozoön into the egg; in *Nereis* they occur before the slow penetration can be completed, or even if the spermatozoön is shaken loose shortly after penetration has begun.

In describing the remarkable transformation undergone by the spermatozoön within the egg it will be convenient to deal with its various parts separately.

**The Nucleus.**—Immediately after gaining entrance to the egg (Fig. 164), the sperm head begins to enlarge and assume the usual form and structure of a nucleus. Meanwhile it advances toward the egg nucleus. As Lillie points out, both nuclei pass toward a position of equilibrium in a cell preparing to divide and consequently meet; the assumption of an attractive force between them is unnecessary. By the time they meet the sperm nucleus has usually, but not always, become equal in size and appearance to the egg nucleus. The union of the two "pronuclei" usually occurs at once. In a great many cases there may be no actual fusion of the nuclei as such. As they come close to one another each passes through the prophase stages and gives rise independently to its group of chromosomes, the two groups arranging themselves in a common spindle which organizes when the nuclear membranes disappear. The nuclei may behave variously in this respect within the same species. In *Strongylocentrotus lividus* Danchakoff (1916) observed three general modes of behavior: (*a*) The chromatic sperm nucleus may be added to the comparatively achromatic egg nucleus, the two forming a common reticulum from which the chromosomes later differentiate; (*b*) the sperm nucleus may become achromatic before uniting with the egg nucleus, the achromatic fusion nucleus forming a reticulum from which the chromosomes develop; (*c*) the sperm nucleus may differentiate its chromosomes before uniting with the egg nucleus, no common reticulum being formed, and the maternal and paternal chromosomes remaining separate throughout their differentiation.

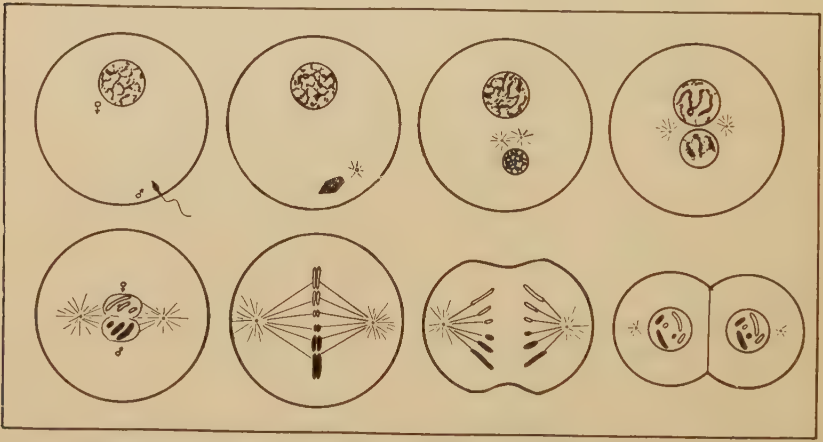

Fig. 164.—Diagram of syngamy and cleavage in an animal. It is assumed in this case that meiosis has been completed before the entrance of the spermatozoön.

In the first cleavage mitosis, whether the gamete nuclei have formed a common reticulum or not, each chromosome undergoes a longitudinal division, the halves passing to the two daughter nuclei. This process is repeated in every subsequent somatic mitosis, so that every somatic nucleus has descendants of every parental chromosome originally present in the fertilized egg. In most animals the first cleavage mitosis is followed by the division of the fertilized egg into two cells (blastomeres), but in some cases there are several free nuclear divisions before any cleavage into cells occurs. In some instances it has been shown that the plane of the first cleavage is determined by the chance point of entrance of the spermatozoön, and that the bilaterality of the embryo bears a direct relation to this cleavage.[1] In other animals, on the contrary, the plane of the first cleavage does not coincide with the plane of bilateral symmetry;

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[1] Wilson and Mathews (1895) on the sea urchin; Just (1912) on *Nereis*. See Morgan (1924*b*).

moreover, some eggs may show such symmetry before fertilization (*e.g.*, many insects).

The more or less independent formation of the maternal and paternal chromosomes without an intimate nuclear fusion before the first cleavage mitosis is known as *gonomery*, and has been observed in both animals and plants (Figs. 160, 164a). Huettner (1924) has recently reported its occurrence in *Drosophila*. Furthermore, in several organisms it has been found that the two parental groups of chromosomes can be distinguished not only in the first embryonal mitosis, but also in several divisions thereafter.[1] This is especially evident in hybrids. There is reason to believe that the chromosomes brought together by the two gametes, although intermingled in the nuclei of the new individual, never actually fuse, unless it is in synapsis at the time of the next meiosis; and it has already been pointed out that synapsis probably represents a process of interchange rather than a fusion (Chapter XIII). The fact that the nuclear elements thus maintain their identity throughout successive life cycles is of the greatest importance in connection with problems of heredity.

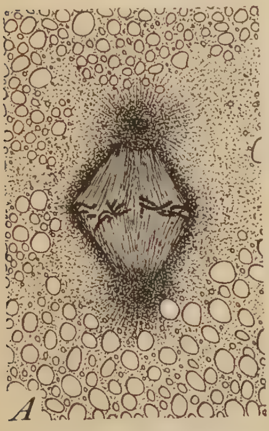

FIG. 164a.—Independence of paternal and maternal chromosomes in the cleavage of the egg of *Cryptobranchus*. *A*, first cleavage. *B*, *C*, prophase and metaphase of fourth mitosis. (*After B. G. Smith*, 1919.)

**The Centrosome.**—Shortly after the entrance of the spermatozoön into the egg, an aster develops in the cytoplasm near the base of the sperm head, and at the focus of the aster a centriole appears (Figs. 162, 164). The inclusion of a spermatid centriole in the middle piece during spermiogenesis and the appearance of the aster and centriole in the general region of the middle piece after fertilization led to the widely accepted view that the newly appearing centriole is, in reality, that of the spermatid. Whatever its origin, it soon divides into two which function in the first cleavage mitosis. These facts had much to do with the formulation of a theory of fertilization set forth by Boveri (1887, 1891), who was much impressed by the conspicuous part played by centrosomes in cell-division. According to Boveri's theory, the egg is not able to undergo division because of the lack of any centrosome to initiate the process, while the spermatozoön has a centrosome but not sufficient cytoplasm in which to act. Through the union of the gametes all the organs necessary for division are brought together and cleavage proceeds. This theory has recently been recalled by Walton (1918) in his work on *Ascaris canis.*

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[1] Rückert (1895) and Haecker (1895) on *Cyclops;* Conklin (1901*a*) on *Crepidula:* B. G. Smith (1919) on *Cryptobranchus.*

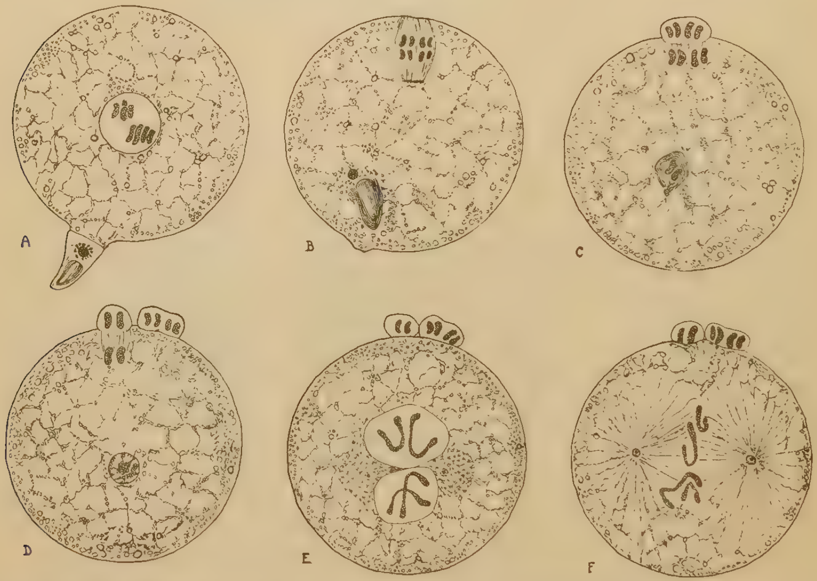

Fig. 165.—Meiosis and syngamy in *Ascaris*. *A*, spermatozoön about to enter egg. *B*, spermatozoön inside; first meiotic division in progress. *C*, first mitosis completed; first polar body budded off. *D*, second meiotic division, forming second polar body; nucleus of spermatozoön below. *E*, meeting of male and female pronuclei, each with 2 chromosomes. *F*, first cleavage mitosis, showing 2 paternal and 2 maternal chromosomes. (*After Hertwig.*)

Various other theories regarding the origin of the cleavage centrioles were propounded, some workers identifying them with those of the egg, and others deriving them from both egg and sperm (see Wilson, 1925, pp. 438*ff*). That either the egg or the sperm centrioles actually persist as such through syngamy and cleavage now seems doubtful. Since the middle piece, presumably with the centriole, does not enter the egg at all in *Nereis,* it has been thought that the male nucleus in some way induces the formation of asters and centrioles by the egg cytoplasm.

Lillie found that even a portion of the sperm head will bring about this effect. It has been shown by Koltzoff (1909), however, that a chromatic rod, which may be an elongated centriole, traverses the sperm head in *Nereis*. In almost every case there are gaps in the known history of the centrioles in syngamy, and it remains to be clearly proved that the cleavage centrioles are continuous with those of either gamete. The fact that the formation of asters with centrioles in the egg cytoplasm can be artificially induced by treating the eggs with certain chemicals, such as weak $MgCl_2$, suggests that the spermatozoön carries a substance which brings about centriole formation in a similar way. However this may be, the importance of the centrosome undoubtedly lies in its relation to cleavage rather than to syngamy.

**Cytoplasm and Chondriosomes.**—In animals, as in plants, the evidence, in general, indicates that the cytoplasm of the male gamete is of relatively little importance in syngamy. A considerable amount of paternal cytoplasm is introduced in some cases (*Ascaris*), but in others none at all can be seen to enter. This is particularly true of such a case as *Nereis*, in which the middle piece and the tail remain outside the egg. These facts are of interest in connection with the theory of Meves and others regarding the significance of chondriosomes. In *Ascaris* Meves (1911) observed that the chondriosomes ("plastochondria") introduced by the spermatozoön surround the male nucleus for a time and then mingle with the chondriosomes of the egg. From this and other observations he concluded that the chondriosomes, which he held to be important agents in differentiation, are responsible for the transmission of certain paternal hereditary characteristics from generation to generation. There are other facts besides the failure of the chondriosome-carrying middle piece and tail to enter the egg which diminish the plausibility of this theory. It has been shown in the bat by Van der Stricht (1902), in the guinea pig by Lams (1913), and in echinoderms by Meves himself (1914*a*) that when parts other than the sperm head enter the egg they show no signs of activity and pass to one daughter cell only at each cleavage division, not being distributed among the cells as would be expected of a material functioning in differentiation or heredity.

One should not lose sight of the fact, however, that cytoplasm and chondriosomes are passed from generation to generation through the egg. As will later be pointed out, much that happens in the embryo depends upon the constitution of the egg cytoplasm. No differentiation occurs without the proper combination of nucleus and cytoplasm, both derived directly from the preceding generation through one or both gametes. The presence of chondriosomes in the egg and sometimes in the sperm probably indicates the occurrence of certain physiological processes as it does in other cells; but, although such processes may influence the course of differentiation within certain limits, there is as yet no adequate evidence that the chondriosomes or any other cytoplasmic constituents act as differential factors of inheritance in any way comparable to the action of nuclear factors.

**Protozoa.**—Much uncertainty prevails with respect to sexual phenomena in Protozoa. A number of early reports of processes which seemed to represent syngamy have turned out to be results of misinterpretation; in fact, it is not at all clear that sexual reproduction exists in many groups of Protozoa (see Kofoid, 1923). Moreover, the significance of other nuclear phenomena which have been more adequately described is not yet understood.

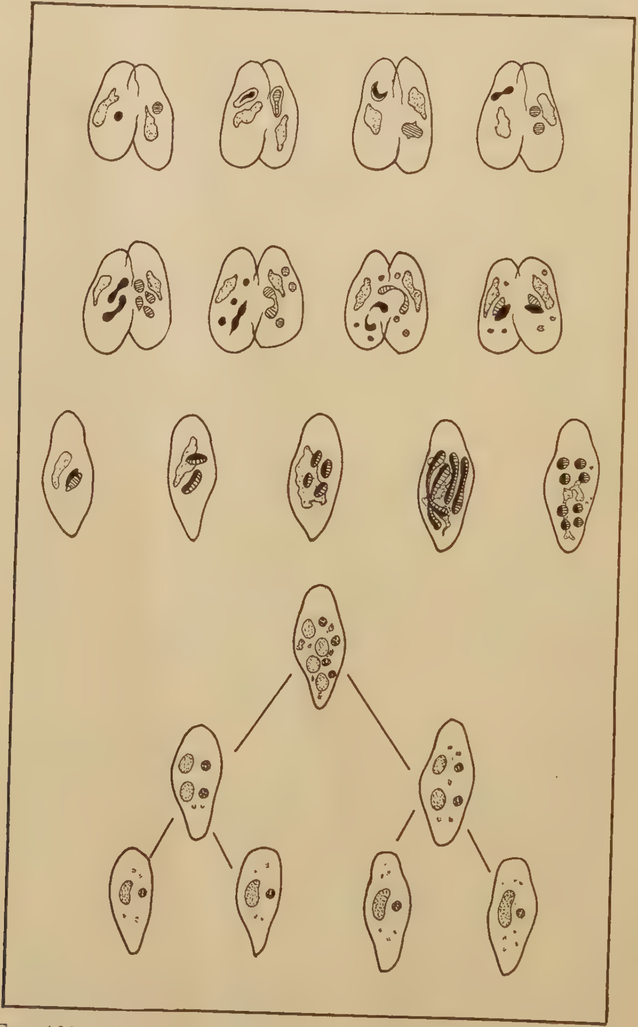

FIG. 166.—Conjugation in *Paramœcium*. (*After Morgan*, 1913.)

One of the best-known cases of nuclear behavior in Protozoa is that occurring at the time of conjugation in the infusorian, *Paramœcium caudatum*, as originally shown by the researches of Maupas (1889) (Fig. 166). To quote from Wilson (1900),

> . . . in *Paramœcium caudatum*, which possesses a single macronucleus and micronucleus, . . . conjugation is temporary and fertilization mutual. The two animals become united by their ventral sides and the macronucleus of each begins to degenerate, while the micronucleus divides twice to form four spindle-shaped bodies. Three of these degenerate, forming the "corpuscles de rebut," which play no further part. The fourth divides into two, one of which, the "female pronucleus," remains in the body, while the other, or "male pronucleus," passes into the other animal and fuses with the female pronucleus. Each animal now contains a cleavage-nucleus equally derived from both the conjugating animals, and the latter soon separate. The cleavage-nucleus in each divides three times successively, and of the eight resulting bodies four become macronuclei and four micronuclei. By two succeeding fissions the four macronuclei are then distributed, one to each of the four resulting individuals. In some other species the micronuclei are equally distributed in like manner, but in *P. caudatum* the process is more complicated, since three of them degenerate, and the fourth divides twice to produce four new micronuclei. In either case at the close of the process each of the conjugating individuals has given rise to four descendants, each containing a macronucleus and a micronucleus derived from the cleavage-nucleus. From this time forward fission follows fission in the usual manner, both nuclei dividing at each fission, until, after many generations, conjugation recurs.

It was for a long time supposed that conjugation involving an intermixture of nuclear material from two individuals was necessary for the continued vigor of the race in such animals, and that without the periodic recurrence of the process the race would become increasingly senescent and finally die out. But the long-continued experiments of Woodruff, Jennings, and others showed that this is not the case. Given a properly regulated environment, these organisms will give rise to thousands of successive generations with no conjugation and with no decline in vigor. The natural conclusion seemed to be that protoplasm does not necessarily become senescent through continued vegetative activity. The problem, however, soon assumed a new aspect.

**Endomixis.**—In 1914 Woodruff and Erdmann made the significant discovery of *endomixis*, a process whereby these organisms periodically undergo a nuclear reorganization without conjugation. In conjugation, as shown above, the micronucleus in each individual initiates a series of three mitoses, one of the resulting nuclei passing as a gamete nucleus to the other individual, where a fusion takes place. Since some of the products of the division of the fusion nucleus become meganuclei, conjugation involves a replacement of the old meganucleus by material from the reserve micronucleus, as well as the exchange and fusion of micronuclei. In endomixis, on the other hand, there is such a replacement, but no exchange or fusion. For example, in *Paramœcium aurelia*, which has two micronuclei, it is found that after every 40 or 50 generations (by fission) the meganucleus disintegrates in the cytoplasm, while each micronucleus undergoes two successive mitoses (rather than three). All but one or two of the resulting nuclei degenerate, those which remain later dividing to produce the new mega- and micronuclei.

The question of whether the race can continue to live without either conjugation or endomixis has awaited answer for several years. In *Paramœcium aurelia* and *P. caudatum* the periodic recurrence of this nuclear reorganization is coincident with a rhythmic acceleration in metabolic activity, which at least in part explains the ability of these animals to maintain their vigor without conjugation. Furthermore, if endomixis ceases, the cultures die. But in other species endomixis takes place in the encysted stage or is lacking altogether, yet the metabolic rhythms occur and the race continues. This indicates some factor other than endomixis as the cause of the periodic acceleration of vital activity. The results of recent researches[1] point to the general conclusion that neither conjugation nor endomixis is necessary for the continued existence of the race, although under environmental conditions inducing senile change both processes have rejuvenating effects.

Endomixis thus resembles syngamy in its stimulative effect on metabolism and development, but its possible relation to variation and heredity is not so clear. There is no evidence that in endomixis there is any meiotic disjunction of chromosomes in the formation of the degenerating nuclei; in fact, there are certain indications that in the process of conjugation disjunction occurs in the third or gamete-producing mitosis, this mitosis being the one which is lacking in endomixis. Molecular rearrangements doubtless occur, but to what extent these may affect the constitution or action of the physical basis of heredity remains for the future to determine.

Similarly problematic are other nuclear phenomena observed in Protista, notably *autogamy*, in which fusions occur between half-nuclei of the same cell, with or without the formation of "reduction nuclei." These phenomena involve many uncertain cytological points, as well as questions of the nature of sexuality which are equally obscure.[2]

**The Physiology of Fertilization.**—The problem of determining the physico-chemical changes involved in the activation of the egg has been attacked through studies of artificial parthenogenesis, as well as through direct analyses of the chemical constitution of the gametes at these stages.[1]

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[1] Woodruff and Spencer (1924), Spencer (1924), E. L. Moore (1924). See especially the convenient summary by Woodruff (1925).

[2] See M. Hartmann (1909, 1914), Erdmann (1920), G. Hertwig (1921), and especially the discussions by Jennings (1920), Kofoid (1923), and E. B. Wilson (1925).

In 1899 Jacques Loeb made the important discovery that the parthenogenetic development of certain animal eggs can be artificially induced. In most cases two successive treatments were found necessary: first, a brief treatment with sea water containing some permeability-increasing substance (certain fatty acids, bases, soaps, alkaloids, glucosides, and foreign blood sera); and, second, a longer treatment with hypertonic sea water, oxygen-free sea water, or sea water with a trace of KCN. The first treatment causes the formation of a fertilization membrane, which seems to be a condition necessary for continued development, the critical change apparently being a momentary increase in surface permeability which sets in motion the developmental reactions; but in most cases the eggs become sickly and die unless given the second treatment. Loeb concluded that the spermatozoön in normal fertilization carries two substances, one of which produces the necessary initial surface changes, even when the spermatozoön fails to enter the egg, while the other in some way acts as does the second treatment in artificial parthenogenesis. Loeb thought that the sickliness of eggs given only the first treatment was due to a continuance of the cytolytic action begun by the first treatment, but F. R. Lillie pointed out the greater probability of the view that it is due to some internal cause, citing as supporting evidence certain cytological phenomena observed by Herlant in eggs activated by Loeb's method.

During the healthy period (12 to 24 hours) immediately following the first treatment Herlant (1917) observed the following changes. After the formation of the membrane and a hyaline zone, the nucleus becomes the seat of a series of conspicuous changes. The nuclear membrane disappears, and around the chromosomes there is formed a monaster (one-poled group of achromatic fibers), but no amphiaster. The chromosomes divide but do not separate, and, although the cytoplasm becomes active, no cytokinesis ensues. The chromosomes then return to the reticulate condition. This process is repeated several times, the nucleus increasing in bulk each time; but it soon becomes very irregular and the egg ultimately breaks down by general cytolysis. The second treatment in some way gives the egg the capacity to divide regularly. Morgan (1899) and Wilson had long before shown that such treatment with hypertonic sea water causes aster formation in the unfertilized sea urchin egg. Herlant showed that one of these asters and a second aster formed in connection with the egg nucleus together form an amphiaster, normal division then ensuing. Thus the breakdown of the egg after the first treatment alone appears to be related to the absence of a proper coördination of nuclear and cytoplasmic division. The second treatment produces a regulatory effect, partly through aster formation, resulting in normal development. This recalls Boveri's centrosome theory of normal fertilization.

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[1] For general accounts, see Loeb (1913), F. R. Lillie (1919), Lillie and Just (1924), and R. S. Lillie (1923).

Among other agencies inducing activation in certain cases may be mentioned high temperature (R. S. Lillie, 1908, 1915), carbon dioxide (Herlant, 1920), puncture by needles, allowing gases or other substances to pass the membrane (Bataillon, 1910, and others), and release from the vitelline membrane (Heilbrunn, 1920*b*). Popoff (1920, 1922) reports remarkable stimulative effects of hypertonic salt solutions on the somatic cells of plants.

*The Fertilizin Theory.*—The best substantiated theory of fertilization at present is that developed by F. R. Lillie (1913, etc.) and supported by Just and others, according to which the egg is an "independently activable system," the spermatozoön contributing neither organs (Boveri) nor substances (Loeb) necessary to activation. "The egg possesses all substances needed for activation; the spermatozoön is an inciting cause of those reactions within the egg system upon which development depends." As a result of his direct analysis of the gametes during the fertilization period Lillie has identified a substance in the egg which he calls *fertilizin*. This substance is present in the egg for a short time only. Its formation usually begins at about the time of the breakdown of the germinal vesicle, from which it probably emanates; and immediately after fertilization its production ceases, possibly through the neutralizing action of a second substance. As a rule, it is only during the brief period when fertilizin is present that spermatozoa will enter the egg. Moreover, membraneless egg fragments without fertilizin are not entered. Hence it seems clear that the entrance of more than one spermatozoön is normally prevented not simply by the mechanical barrier of the fertilization membrane which develops when the first sperm enters, but chiefly by the physiological state of the egg protoplasm.

Fertilizin has two effects: it first acts by causing an agglutination of the spermatozoa at the surface of the egg, and later causes the activation of the egg. It may thus be said to stand between the spermatozoön and the activation reactions in the egg. Being present in the egg secretion at a certain period it binds the spermatozoön to the surface of the egg, and the spermatozoön, without necessarily penetrating the egg at all, releases the activity of the fertilizin within the egg, which results in development. In brief, the activating substance is already present in the egg and is not brought to it by the spermatozoön. It may be incited to activity by the spermatozoön, but by other agencies as well.

It is the opinion of Glaser (1921) that the activating agent in the egg secretion is not a single substance with two side chains, but a pair of substances. In the case of *Arbacia* Woodward (1918) isolated a lipolysin, which acted as a parthenogenetic agent but did not agglutinate the spermatozoa, and a second substance which produced just the contrary effects. Glaser has studied the egg secretions of a number of other animals, and has also concluded that two substances are present: a *lipolysin*, an enzyme inducing parthenogenetic development, and an *agglutinin*, also possibly an enzyme, which binds the spermatozoa to the egg. He does not think that these are simply due to the splitting of fertilizin.

Among other immediate physiological consequences usually following fertilization may be mentioned an increase in permeability to oxygen, $CO_2$, pigments, water, alkalis, vital dyes, and certain other substances; an increase in the rate of oxidation; an increase in viscosity, centering in the sperm aster; a rise in electrical conductivity; and the loss of fertilizin. (Lillie, 1919). Just (1920) points out that the alterations in viscosity, permeability, and rate of oxidation are not incident to the fertilization reaction *per se*, but are primarily changes bound up with the egg's division. Such changes occur in other cells also, and do not explain the activation of the egg.

In this connection one may be cautioned against the assumption that activation is complete when the spermatozoön has gained entrance to the egg. Morgan (1924*f*) cites the fact that if an inseminated egg be cut into two pieces in such a way that one fragment contains the egg nucleus and the other the sperm nucleus, only the latter develops; and he therefore emphasizes the inadequacy of theories of fertilization which terminate with the entrance of the spermatozoön.

**Conclusion.**—As pointed out at the beginning of the chapter, syngamy should always be conceived as a mutual process: that which undergoes development following syngamy is a zygote—the fusion product of two gametes, no matter how dissimilar these may have been in their morphological and physiological differentiations. The fact that the nuclear contributions of the two gametes are in general equivalent in all types of normal syngamic union is one of cardinal importance, especially in connection with the nuclear theory of heredity. Subsequent chapters will deal at length with the manner in which the periodic reorganization of the nuclear mechanism through meiosis and syngamy is correlated with the recombination and transmission of heritable characters. It will then be apparent that syngamy may be concerned not only with the continuance of the race, but also with its gradual modification through successive generations.

# CHAPTER XVI

## APOMIXIS AND RELATED PHENOMENA

The many known kinds of reproduction in organisms are ordinarily grouped in two main categories, sexual and asexual. In the latter category are several modes which seem clearly to represent aberrations or derivatives of the sexual process, in that they involve the structures commonly concerned in sexual reproduction. These peculiar phenomena play a considerable rôle, sometimes even an exclusive one, in the reproduction of many organisms, and must often be taken into account in interpreting hereditary behavior.

It is convenient to make use of the following classification of reproductive processes: *amphimixis,* in which the individual arises from the fusion product of two gametes, as already described in the preceding chapter; *apomixis,* in which there is no sex act whatsoever, a condition which may be autonomous or artificially induced; and two other categories including cases of doubtful homologies and variously treated by different authors: *pseudomixis,* whereby a new individual or phase of the life cycle arises from the fusion product of two protoplasts not specifically differentiated as gametes, and *parthenomixis,* in which it arises as the result of a fusion of nuclei produced within one gametangium or gamete.

In the present chapter attention will be devoted chiefly to apomixis in its two principal forms, parthenogenesis and apogamy. The first of these occurs in both animals and plants, and the second in plants only. A condition related to apogamy, namely, *apospory,* will also be considered.

### PLANTS

The life cycle in bryophytes and vascular plants is characterized by a regular alternation of two well-marked phases or generations: the *gametophyte,* which arises from the spore and produces gametes; and the *sporophyte,* which arises from the fusion product of two gametes and produces spores. In such a normal life cycle the number of chromosomes in the nuclei is doubled by the union of the gametes and reduced to the original number at sporogenesis; the gametophyte is therefore the haploid generation and the sporophyte the diploid generation, the limits of the two being marked by the cytological crises, syngamy and meiosis. Such an alternation of haploid and diploid phases has been discovered in the life cycles of certain thallophytes also, so that the general conception of alternation of generations has been extended to them. This, however, is not the place for a discussion of the homologies implied.[1]

It is important to bear in mind that the correlation between alternation of generations and alternation of nuclear phases differing in chromosome number is not universal and invariable. Many cases are known in which the life cycle shows the two generations as usual, but with no changes in the number of chromosomes, as will be seen in the following pages. The causes of alternation include something more fundamental than mere chromosome number.

The known cases of apomixis and related phenomena are too numerous and varied to be described in a single chapter. In the following pages is presented little more than a classification of the principal types of behavior which occur, with citations of a few of the best-known illustrative examples.[2]

**Apomixis.**—No sexual fusion.

A. Parthenogenesis.—The development of a sporophyte from a female gamete (or sometimes a male gamete?) without syngamy.

1. *Haploid parthenogenesis:* The egg is haploid.[3]

[Called haploid parthenogenesis by Hartmann (1909) and Renner (1916); generative parthenogenesis by Winkler (1904, 1908, 1920); true parthenogenesis by Strasburger (1907).]

The occurrence of haploid parthenogenesis in vascular plants is extremely rare. Haploid eggs have been observed to undergo mitosis in *Gastrodia* (Kusano, 1915) and *Œnothera* (Haberlandt, 1921, 1922), but no fully developed haploid angiosperms are known except in *Datura* (Blakeslee, *et al.*, 1922) and probably *Nicotiana* (Clausen and Mann, 1924). The origin of these is in doubt, but the genetic evidence indicates strongly that in *Datura* haploid eggs have developed.

In the algæ this mode of development probably occurs more often. In *Fucus* the development of the unfertilized egg has been induced by artificial means (J. B. Overton, 1913), but the cytological facts are here unknown. Motile gametes of certain other algæ have been observed to develop without conjugation, as in *Ectocarpus* (Kylin, 1918). It is not improbable that haploid development occurs in the case of the "parthenospores" of *Spirogyra* (see Ernst, 1918). In *Vaucheria* ( von Wettstein, 1920) the contents of either the oögonium or the antheridium may be made to regenerate a new individual; what is virtually "male parthenogensis" occurs in the latter case.

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[1] See Tansley (1912), Bonnet (1914), Buder (1916), Kylin (1916*b*), Renner (1916), Fritsch (1916), B. M. Davis (1916), and Svedelius (1921).

[2] The classification here employed follows, in the main, that drawn up by Winkler (1908, 1920), with certain modifications, chiefly in terminology, suggested by M. Hartmann (1909). We have endeavored to put the student in touch with the many terms employed by various other authors by including them in brackets under each heading. For discussions of the phenomena treated in this chapter, some of them with classifications of cases, see Winkler (1908, 1920), Strasburger (1909*b*), Ernst (1918), Renner (1916), Hartmann (1909), Prell (1923*b*), Vines (1911), P. Hertwig (1920*a*), and Tischler (1921–1922, pp. 493*ff*). See Tischler for thallophytes especially, and Hartmann for thallophytes and Protozoa.

[3] By "haploid" is here meant the reduced number of chromosomes for the plant under consideration. In tetraploid plants the reduced number is in reality the diploid number on the basis of the fundamental number characteristic of the species or genus.

2. *Diploid Parthenogenesis.*—The egg is diploid.[1]

[Called diploid parthenogenesis by Hartmann and Renner; somatic parthenogenesis by Winkler; oöapogamy by Strasburger, Juel, and Ernst; and parthenapogamy by Farmer and Digby (1907).]

A considerable number of cases of diploid parthenogenesis are known among vascular plants: *Marsilia Drummondii* (Strasburger, 1907); *Athyrium filix-fœmina*, var. *clarissima* and *Scolopendrium vulgare* (Farmer and Digby, 1907); *Alchemilla* (Murbeck, 1901; Strasburger, 1905*b*; Böös, 1917, 1920); *Antennaria alpina* (Juel, 1898, 1900); *Archieracium* (Rosenberg, 1906, 1917; Ostenfeld, 1910, 1912); *Atamosco texana* (Pace, 1913); *Erigeron annuus* (Tahara, 1915, 1921; I. Holmgren, 1919); *Eupatorium glandulosum* (Holmgren); *Calycanthus* (Schürhoff, 1923); *Taraxacum* (Murbeck, 1904; Juel, 1904; 1905; Osawa, 1913; Sears, 1917, 1922; Stork, 1920*a*); *Chondrilla* (Rosenberg, 1912); *Wikstrœmia* (Winkler, 1906; Strasburger, 1909*a*); *Allium odorum* (Haberlandt, 1923), and other cases. It also occurs in *Chara crinita* (Ernst, 1918, 1921).

The diploid state of the egg is due to a failure of the meiotic process. The two sporocyte divisions may occur, however (*Marsilia*), or only one of them may occur (*Taraxacum*, *Chondrilla*), or no quartet at all may be formed (*Antennaria alpina*, *Atamosco*, *Archieracium*, *Eupatorium*, etc.). Sporogenesis without haplosis is sometimes called *apomeiosis*.

B. Apogamy.—The apomictic development of a sporophyte from a cell or cells of the gametophyte other than the gamete is called apogamy.

1. *Haploid Apogamy.*—The developing cells have haploid nuclei.

[Called haploid apogamy by Hartmann, generative apogamy by Winkler, haploid apogamety by Renner, and meiotic euapogamy by Farmer and Digby.]

The development of sporophytes from vegetative tissue of gametophytes with the reduced chromosome number and without nuclear fusion has frequently been observed among ferns, but no case is known in the angiosperms. It has been reported in *Lastrœa pseudo-mas*, var. *cristata-apospora* by Farmer and Digby (1907), and in *Nephrodium hirtipes* by Steil (1919). The process usually begins with the division of the gametophyte cells to form a meristematic mass of "engrafted tissue," which then grows into a new sporophyte (Fig. 167). Ordinarily, apogamy is offset in the life cycle by apospory, but in *Nephrodium hirtipes* the spores are formed, though in an abnormal manner. When there are eight sporogenous cells in the sporangium there is an incomplete nuclear division, each nucleus coming to have the diploid number of chromosomes. These eight diploid cells then function as sporocytes and produce 32 haploid spores (Fig. 168, *B*).

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[1] In polyploid forms this number might be actually tetraploid, hexaploid, octoploid, or some other multiple. "Diploid" here means simply the unreduced number for the plant in question.

The propriety of regarding the foregoing cases as examples of haploid apogamy has been questioned. The sporophyte arises from cells with the reduced chromosome number, but this may not be a haploid number in the strict sense. That *Lastræa* and *Nephrodium* are polyploid forms and therefore have gametophyte nuclei which are at least diploid has been suggested by Gates (1909) and Ernst (1918), so that the actual occurrence of *truly* haploid apogamy is doubtful (P. Hertwig, 1920).

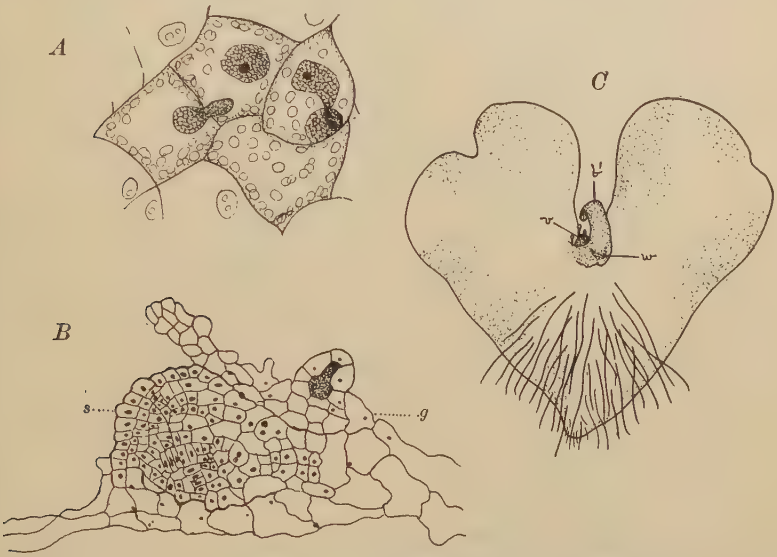

Fig. 167.—*A*, nuclear migration in gametophyte cells of *Lastræa pseudo-mas* var. *polydactyla*. (*After Farmer and Digby*, 1907.) *B*, section through gametophyte, showing young sporophytic tissue (*s*) "engrafted" into surrounding gametophytic tissue (*g*). (*After Farmer and Digby*.) *C*, sporophyte arising apogamously from gametophyte in *Pteris cretica: b'*, first leaf; *v*, stem apex; *w*, root. (*After de Bary*.)

2. *Diploid Apogamy*.—The developing cells have diploid nuclei.

[Called diploid apogamy by Hartmann, somatic apogamy by Winkler and Ernst, diploid apogamety by Renner, and euapogamy by Farmer and Digby.]

The development of a sporophyte from diploid cells of the gametophyte other than the egg has been observed in several angiosperms: *Antennaria alpina* (Juel), *Alchemilla sericata* (Murbeck; Böös), *Burmannia* (Ernst and Bernard), *Archieracium* (Rosenberg), *Allium odorum*

(Tretjakow, 1895; Hegelmeier, 1897, 1901; Haberlandt, 1923). The cells so developing may be synergids (*Antennaria, Alchemilla, Burmannia*), and also antipodals (*Allium*). Reported cases of the similar behavior of polar nuclei and endosperm cells are open to grave doubt.

C. Sporophytic Budding.—The formation of sporophytes by diploid cells surrounding the embryo sac, which project into the sac and develop into embryos. Commonly the cells in question belong to the nucellus ("nucellar embryony"), but often they are integument cells.

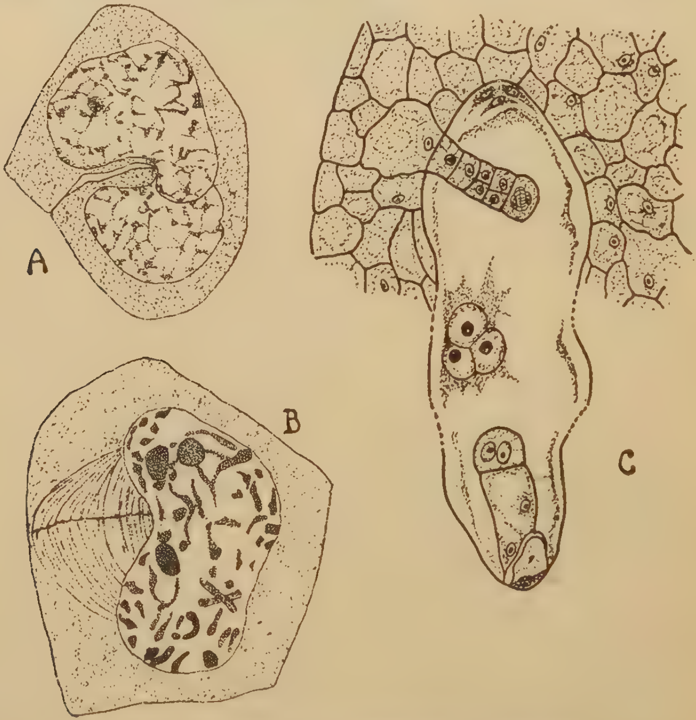

Fig. 168.—*A*, nuclear abnormality in sporangium of *Aspidium falcatum*. (*After R. F. Allen*, 1911.) *B*, incomplete nuclear division in sporangium of *Nephrodium hirtipes*. (*After Steil*, 1919.) *C*, diploid parthenogenesis and sporophytic budding in the embryo sac of *Alchemilla pastoralis:* the egg is developing below and a cell of the nucellus is forming an embryo above; two polar nuclei and one synergid nucleus at center. (*After Murbeck*, 1901.)

This process occurs in a number of angiosperms, commonly in species which show also parthenogenesis or apogamy (Fig. 168, *C*). The nuclei of the sac into which the new embryos project may be either diploid (*Funkia*) or haploid (*Citrus, Allium, Poa, Hieracium*). Embryos may arise from the egg, other gametophytic cells, and sporophytic cells in the same plant, the condition known as polyembryony often resulting. In genetic researches the exact mode of origin of extra embryos is a matter of considerable moment.

It is obvious that this formation of new sporophytes as buds from tissue of the old one cannot be very sharply differentiated from the more ordinary types of *vegetative propogation;* in fact, Winkler treats vegetative propogation as a case of apomixis. Hartmann, on the contrary, includes under apomixis only those modes of reproduction which seem to have been derived from the sexual process in some way, or which involve structures usually concerned in sexual reproduction. In general, this distinction between apomixis and vegetative propogation is a convenient one, although both are cases of asexual reproduction, and although the derivation of the asexual process is in many cases obscure.

**Pseudomixis.**—The development of an individual or distinct phase of the life cycle from the fusion product of two protoplasts not specifically organized as gametes.

[Called pseudomixis by Winkler, pseudogamy by Hartmann, and somatogamy by Renner.]

Here are included a number of peculiar phenomena which it is difficult to homologize fully with regular modes of sexual behavior. The fusion may occur between two vegetative cells, as in *Lastrœa pseudo-mas*, var. *polydactyla* (Farmer and Digby, 1907). In this fern the nuclei of certain gametophyte cells were observed to pass through the wall into adjacent cells, where nuclear fusions occurred; a group of diploid cells ("engrafted tissue") then appeared in this region and developed into a sporophyte (Fig. 167, *A*, *B*). In certain ascomycetes it has been claimed that a nuclear fusion occurs in the vegetative hyphæ, and that ascogenous hyphæ then arise from the fusion product; this claim, however, has not been well substantiated (see p. 325). Some authors would include here also the fusion occurring at the base of the æciospore sorus in the Uredineæ, especially certain cases in which one of the fusing cells is vegetative. The propriety of this procedure depends upon the interpretation given the basal cells; the line between gametes and fusing cells "not specifically organized as gametes" is one which cannot be sharply drawn.

**Parthenomixis.**—The development of a new individual or a distinct phase of the life cycle as the result of the fusion of two nuclei produced within one gametangium or gamete.

[Called parthenomixis by Winkler, and parthenogamy by Hartmann and Renner.]

A number of cases of this kind have been described among the Protozoa, but among plants the only supposed examples are afforded by certain ascomycetes in which fusions have been reported to take place between the nuclei of the same archicarp in the absence of a functional antheridium. That such a fusion occurs, however, is very doubtful (see p. 325).

It is scarcely possible to make a complete and logical classification of the many reproductive processes which fall within neither of the two principal categories: ordinary amphimixis and apomixis. We have mentioned pseudomixis and parthenomixis, but other classes may be distinguished, particularly among the Protista (see Hartmann, 1909). Knowledge of the curious life cycles there observed is of great importance in connection with many biological problems, but the abnormal phenomena which the student should first fix clearly in mind are those classified above under the head of apomixis.

**Apospory.**—The development of a gametophyte from a cell (or cells) other than a spore is known as apospory. Here should be included only cases in plant groups normally developing gametophytes from spores; thallophytes having no spores in the life cycle are not "aposporous" in the present sense.

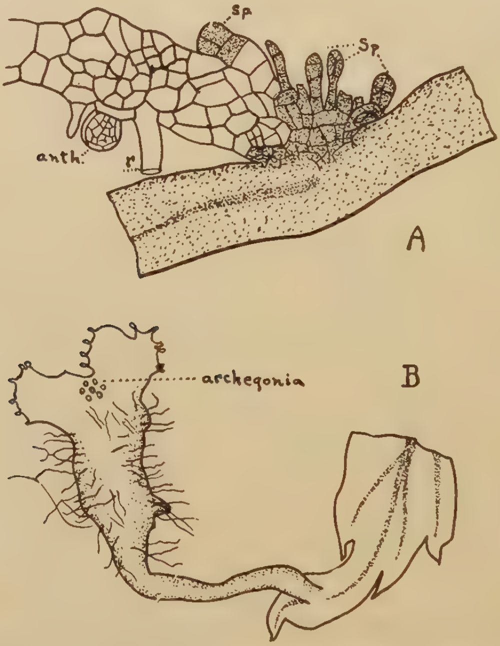

Fig. 169.—*A*, gametophyte with antheridium and rhizoids arising aposporously from tissue of sorus in *Polystichum angulare* var. *pulcherrimum; sp.*, sporangia. *B*, gametophyte with archegonia arising from tip of pinnule in *Polystichum*. (*After Bower*.)

1. A diploid gametophyte arises from a diploid sporophyte.

This form of apospory is of frequent occurrence among ferns. In a number of genera (*Athyrium, Polystichum, Scolopendrium, Lastræa, Pteris, Asplenium*) gametophytes develop as buds from the sporophyte, commonly from the leaf margin and the meristematic tissue at the base of the sorus ("marginal" and "soral" apospory; Fig. 169). Likewise, in several genera of mosses (*Mnium, Bryum, Phascum, Amblystegium*) it has been found possible to induce the development of diploid gametophytes from portions of the sporophyte placed under appropriate cultural conditions (Él. and Ém. Marchal, 1909, 1912; Schweizer, 1923). In some cases these diploid gametophytes produce diploid gametes, which fuse and give rise to tetraploid sporophytes bearing diploid spores. In *Amblystegium* a tetraploid gametophyte has been obtained. Von Wettstein (1924) reports the production of octoploid gametophytes in certain intergeneric hybrids.

Apospory may also occur in angiosperms. In *Hieracium flagellare* Rosenberg (1907*a*) observed the formation of a normally appearing but diploid female gametophyte from a cell of the nucellus or integument. It is conceivable that through further simplification of such a process the nucellar cell might become an egg or embryo initial directly, nucellar embryony thus being an ultimate result of apospory (Ernst).

2. A haploid gametophyte arises from a haploid sporophyte. This is a possibility, but no case is known.

3. A third category is sometimes distinguished as "pseudapospory," since spores may be formed but without haplosis (*apomeiosis*), the gametophyte then arising from the diploid spore. This is known to occur in *Marsilia Drummondii* (Strasburger, 1907). Reported cases in angiosperms are in need of confirmation.

The association of apospory with apogamy in the life cycle is very close; in fact, diploid apogamy would seem to require the previous occurrence of either apospory or apomeiosis. The primary disturbance in the usual course of the life cycle probably arose at the time of sporogenesis in some aberration of the meiotic process (Winkler). The case of haploid apogamy with apospory is less clear, especially in view of the doubt concerning true haploidy in such cases (p. 351). It is possible that in such life cycles sexuality was first lost, and that irregularities in sporogenesis followed (Renner).

**The Causes of Apomixis.**—It is a noteworthy fact that apomictic plants are characterized by various irregularities in sporogenesis. The megasporocyte, for example, may form a quartet of diploid spores (*Marsilia*), a pair rather than a quartet (*Taraxacum*), or no spore cells at all (several genera). Similar irregularities in microsporogenesis lead to the production of varying numbers of functionless pollen grains, or even to the complete lack of pollen. Such facts strongly suggest some aberration of meiosis.

Cytological studies have shown that the chromosomes do exhibit striking aberrations in behavior at the time of sporogenesis in apomictic plants. In the megasporocyte of *Marsilia Drummondii* the chromosomes undergo synaptic pairing, but then dissociate and split longitudinally as in a somatic mitosis (Strasburger, 1907). In *Antennaria* the meiotic phenomena are fewer, and the mitosis passes sooner into the vegetative form (Strasburger, 1905). In *Wikstrœmia* there is no trace of a synaptic association, the mitosis being purely vegetative in character; here only two cells are formed (Strasburger, 1909). Finally, in *Elatostema sessile* there are no meiotic phenomena and no cell-division; the sporocyte forms the female gametophyte directly (Modlewski, 1908; Strasburger, 1909). These cases illustrate a series of transitional conditions between normal meiosis associated with sexuality, and the failure of meiosis associated with apomixis. A similar series in animals will later be pointed out.

The situation is better known in microsporogenesis, where a series of increasingly aberrant modes of chromosome behavior may be seen within a single genus, notably in *Hieracium* (Rosenberg, 1917). In *Hieracium pilosella,* which is not apomictic, normal synapsis and disjunction are constant in both megasporocytes and microsporocytes. In *H. boreale* synapsis is incomplete, the mitosis being disjunctional for only some of the chromosomes. In *H. lævigatum* and *H. lacerum* there is little or no synapsis, but the chromosomes assume the shortened form characteristic of the meiotic phase, and are irregularly distributed in the first mitosis and equationally split in the second. This "half heterotypic" form of mitosis has been seen also in *Taraxacum* (Osawa, 1913), *Eupatorium* (I. Holmgren, 1916), and *Erigeron* ♂ (Tahara, 1915; Holmgren, 1919). Finally, in *H. pseudoillyricum* and in *Erigeron* ♀ (Holmgren) there is neither a synapsis nor a shortening of the chromosomes: they all split longitudinally, and the single mitosis which occurs is purely equational. Sometimes only one division occurs in *H. lævigatum* also. In the species *boreale, lævigatum,* and *pseudoillyricum,* all of which belong to the subgenus *Archieracium,* are seen three stages in the transition from normal meiosis with sexual reproduction, such as occurs in *H. pilosella,* to ameiotic sporocyte divisions with apomixis. These cases show clearly that there is a connection of some sort between apomixis and a weakness or absence of the synaptic attraction between homologous chromosomes.

Another notable fact is the common association of apomixis with polyploidy. When the chromosome number of an apomictic species is compared with that of a nearly related sexual species, it is found in most cases that the former is larger. In about one-half of the known cases in angiosperms the apomictic species have twice the numbers found in the related sexual species—they are tetraploid; and in some cases the multiple is still larger. On the contrary, a number of apomictic plants are known which have the same number as the sexual species, and in at least one case the former has but half as many chromosomes as the latter. In spite of these exceptions, however, the correlation of apomixis with polyploidy is rather high, and is doubtless of considerable significance.[1] Furthermore, polyploid forms, like apomictic forms, are often characterized by conspicuous irregularities in chromosome behavior at the time of meiosis. A common cause underlying meiotic irregularity, polyploidy, and apomixis has consequently been sought.

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[1] A table comparing the chromosome numbers of apomictic and sexual species is given by Ernst (1918, p. 321).

That the primary cause of these chromosome aberrations, together with the associated substitution of apomictic for sexual reproduction, is *hybridization*, is a theory which has been proposed by Ernst (1917, 1918) and ably supported by a number of students of such phenomena (Rosenberg, 1917; Winge, 1917; I. Holmgren, 1919; Täckholm, 1920, 1922; and others). The phenomena in question are so exactly paralleled in hybrids of known origin that little doubt can be entertained regarding the essential correctness of the theory, though of course the limits of its application cannot at present be stated.

The importance of deficient synapsis in bringing about polyploidy and apomixis has been emphasized by Winge in a special hypothesis involving the synaptic reaction. It is first supposed that the chromosomes of diploid organisms must act harmoniously in pairs if development and reproduction are to proceed normally. In apomictic forms with the same chromosome number as the nearly related sexual forms, the "pair action" of the chromosomes contributed by the two gametes is sufficiently harmonious for the development of the zygote into a sporophyte, but not for complete synapsis in the sporocytes; meiosis therefore fails, and the diploid gamete may develop apomictically. On the other hand, in apomictic forms with twice as many chromosomes as the related sexual species the pair action is insufficient for the development of the zygote; each chromosome may divide longitudinally, the tetraploid number of chromosomes so formed then showing the pair action necessary for the development of the sporophyte. If the newly formed pairs act harmoniously through meiosis in the sporocytes the result may be a tetraploid form reproducing sexually with diploid gametes; whereas, if meiosis fails through insufficient synaptic reaction, the result may be an apomictically reproducing tetraploid form.

Such sexual sterility, so common in hybrids and polyploid forms, is accordingly regarded as chiefly a result of the inharmonious action of ancestral elements of unlike origin; indeed, it is highly probable that many apomictic forms have arisen through the crossing of normally sexed forms, as Ernst maintained. Apomixis and polyploidy are often associated results of a common cause: the inharmonious synaptic action of chromosomes brought together by hybridization.

This conclusion is supported not only by tetraploid forms, but also by those with other multiples. The cytological features of triploid apomictic forms of *Hieracium umbellatum*, *Erigeron*, and *Eupatorium* indicate that these have arisen through the crossing of diploid and tetraploid forms, according to Rosenberg (1917) and I. Holmgren (1919). Triploidy of itself may not be a proof of hybridity, since it may arise through dispermy, according to Winkler. This objection to the hybridization theory will not apply to the apomictic forms in the *Caninæ* section of the genus *Rosa*, as shown by Täckholm (1920, 1922) and Blackburn and Harrison (1921). In this section are tetraploid, pentaploid, and hexaploid forms, yet at synapsis in all of them only seven gemini are formed, indicating an origin through crossings of diploid forms (14 chromosomes) with forms having higher numbers. (Winge's pair action hypothesis is not applicable to these examples, unless in the case of the origin of the first high-numbered parent form.) Ernst's hybridization theory receives strong support in these apomictic roses. Another bit of evidence is seen in the case of *Chara crinita* (Ernst, 1918, 1921), which, in addition to sexual haploid plants, shows also larger, obligately parthenogenetic diploid plants, the latter being found only where other species of *Chara* are present.

Ernst has applied his theory very widely. Not only does he see in hybridization the initial cause of parthenogenesis, apogamy, apospory, nucellar embryony, and polyembryony,[1] but also holds it to be chiefly responsible for parthenocarpy, reproduction by special vegetative structures such as bulbils,[2] and the exclusive occurrence of vegetative reproduction in certain plant groups. Others are disinclined to attribute all of these phenomena to hybridization as a direct cause, though they hold it likely that hybridization may be indirectly responsible in releasing factors tending to produce such phenomena by forming the proper factorial combination, or in causing disturbances in meiosis which leave the egg diploid (Rosenberg; Holmgren). Neither Ernst nor the other advocates of the hybridization theory hold hybridization to be the sole cause of apomixis. There is considerable evidence that sexual sterility with apomictic development may also be the outcome of nutritive disturbances set up by other causes, such as abnormal cultural conditions, parasitism and wounding. The cells involved in sexual reproduction seem to be especially sensitive to unfavorable environmental influences, and can easily be made to undergo abnormal development or degeneration. In *Œnothera*, Haberlandt (1921, 1922) finds that wounding brings about the formation of adventitious embryos, and attributes this to the action of a wound hormone originating in the injured tissue. He suggests that the similar production of "necrohormones" in normally degenerating cells of the embryo sac, the tapetum, or the neck canal cells of pteridophytes may be responsible for natural apomictic development in vascular plants. But all such development in angiosperms cannot have such a cause, since in certain cases (*Hieracium flagellare*) the apomictic process begins while the original embryo sac is still normally healthy: a nucellar or integumentary cell crowds out this sac and develops a sac itself (Rosenberg). As for apospory in the mosses studied by the Marchals, it seems clearly to have been the result of unusual cultural conditions and their attendant cytological disturbances, no hybridization being involved.

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[1] A classification of cases of polyembryony in angiosperms is given by Ernst (1918, p. 436). See also Coulter and Chamberlain (1903).

[2] *E.g.*, in *Cardamine bulbifera* (Schwarzenbach, 1922).

The developmental capacities of diploid eggs of different origins further suggest hybridization as an important cause of parthenogenesis. Although it has been thought that an unreduced egg develops alone simply because it is diploid (Strasburger, 1910), it is now evident that diploidy *per se* is not the cause. Thus in the Marchals' mosses and in Winkler's (1916) artificially induced tetraploid *Solanum* the diploid eggs will not develop unless syngamy occurs. There is a strong suspicion that this is connected with the non-hybrid constitution of their chromosome complements, and that the parthenogenetic development observed in many other diploid eggs is due to the hybrid origin of their complements. Hence it seems highly probable that heterozygosis is a potent factor in determining the capacity for parthenogenetic development.

In spite of the variety of evidences tending to show a close relationship between hybridization and unusual types of reproductive behavior, it is well to be warned against attributing all cases of pollen abortion and apomixis to any one cause. Irregularities in pollen development are frequently found in plants showing perfect regularity in the development of megaspores and female gametes. This seems to be either an expression of a tendency toward intersexuality, or an effect of some condition peculiarly detrimental to maleness. Certain cultivated plants exhibit such disorders to a marked degree. In many cases, moreover, vegetative reproduction is coupled with normal sexuality. Hence it is probable that many plants are reproducing solely by asexual means not because they have developed the ability to do so as a result of the loss of sexuality, but simply because they were already reproducing in part by such means before sexual derangements set in, and have therefore been able to survive.

## ANIMALS

The natural development of an egg without having united with a male gamete is a phenomenon which is apparently of much more frequent occurrence in animals than in plants. The best known examples are found among the rotifers, crustaceans, and insects, parthenogenesis being the regular mode of reproduction in some species. Other modes also usually occur in such organisms under certain conditions or after a certain number of generations. Some species produce parthenogenetic and zygogenetic eggs which show conspicuous structural differences. Moreover, as has already been described in the preceding chapter, parthenogenesis may be artificially induced in the eggs of other animal groups, notably echinoderms, mollusks, and amphibians, and around this fact centers much of the significant work of modern experimental biology.

It is to be noted that in all of these groups it is the gamete that develops; there is no gametophyte in animals, and therefore no apogamy. Ordinary vegetative reproduction is, of course, common.

In commenting upon parthenogenetic development, Minchin (1912, p. 137) points out that " . . . the gamete which has this power is always the female; but this limitation receives an explanation from the extreme reduction of the body of the male gamete and its feeble trophic powers, rendering it quite unfitted for independent reproduction, rather than from any inherent difference between the two sexes in relation to reproductive activity."

It is necessary to distinguish first of all between *true parthenogenesis* and a number of other phenomena which may be termed *false parthenogenesis*, the latter class corresponding more or less closely to the cases in plants treated under the head of Parthenomixis.[1]

**True Parthenogenesis.**—The development of an egg without syngamy or other nuclear fusion. This is called apomictic parthenogenesis by Prell.

A. *Haploid parthenogenesis:* The egg is haploid. [Called azygoid parthenogenesis by Prell.]

Two maturation divisions occur, with reduction in chromosome number.

The type case of this category has long been the honey bee, *Apis mellifica.* Here two polar bodies are formed as usual, and the haploid egg (16 chromosomes) develops into a drone. Fertilized eggs give rise to female workers. Such haploid parthenogenesis is also reported in a fly (*Trialeurodes vaporariorum*) and a mite (*Tetranychus bimaculatus*) by Schrader (1920, 1923*c*). In a gall-fly (*Neuroterus lenticularis*) the maturing egg in one class of cases gives off two polar bodies, retains the reduced number of chromosomes (10), and develops parthenogenetically into a male fly (Doncaster, 1910–1911). In *Hydatina senta* the eggs giving off two polar bodies with a reduction of the chromosome number from 12 to 6 develop parthenogenetically into males (Whitney, 1909; A. F. Shull, 1921).

Although it has been clearly established in many cases that both haploid and diploid animal eggs can be made to begin development by a variety of treatments, the power of the haploid individuals to continue their development to sexual maturity has frequently been questioned. It was at one time generally thought (Delage *et al.*) that a restoration of the diploid number was necessary for full development, but the work of Boveri seemed to show that one complete haploid set was sufficient. Investigators have repeatedly found, however, that the larvæ of echinoderms, insects, amphibians, and other animals, whether produced by inducing the parthenogenetic development of haploid eggs or by causing the insemination of enucleate egg fragments, soon show a characteristic inability to continue with their metamorphosis and usually die long before sexual maturity is reached.[1] Moreover, it has been found in several cases that larvæ arising from haploid eggs have the diploid number of chromosomes, though the manner in which the doubling occurs is unknown. This is the case in frogs induced to develop by artificial parthenogenesis (G. Hertwig, 1918; Parmenter, 1920; Goldschmidt, 1920*b*). Tauson (1924) reports that in *Asplanchna* the doubling occurs in some way before the first cleavage.

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[1] We shall here follow the classification given by Prell (1923) with certain modifications. See the discussion by Wilson (1925).

In the opinion of P. Hertwig, there is no certain case of complete development with the haploid chromosome number; and she thinks that the classic instances of parthenogenesis in the hymenoptera should be critically reëxamined to determine whether or not the chromosome complement actually is haploid in the strict sense. The uncertainty with respect to the supposed cases of haploid apogamy in plants has already been pointed out (p. 351). It is not improbable that such apogamous fern sporophytes, although they have the "reduced" number of chromosomes, are diploid rather than truly haploid. *Datura* on the other hand, seems to afford an unequivocal case of the complete development of a haploid sporophyte. The haploid set here consists of 12 chromosomes with an odd number in four of the six size classes. The haploid plant is somewhat less vigorous than the diploid, but the haploid number is retained through to the production of functional gametes (Blakeslee *et al.*, 1922). In *Tetranychus* also the evidence appears to indicate that the haploid number (three) is retained to sexual maturity (Schrader, 1923*c*). It seems probable that the weakness of haploid embryos from whole eggs may be due to improper quantitative relations of nucleus and cytoplasm, as Morgan suggests; and that the disturbed equilibrium, although it may not prevent full development in some cases, usually leads either to a regulatory division process whereby the proper relations are restored, or to death.

B. *Diploid parthenogenesis:* The egg is diploid. [Called zygoid parthenogenesis by Prell.]

1. There are no maturation divisions, and no reduction in chromosome number.

This mode of behavior occurs in one known example, *Neuroterus lenticularis* (Doncaster, 1910, 1911, 1916). In certain eggs of this gall-fly the nucleus approaches the surface of the egg as if to produce a polar body, but returns to the middle of the egg and divides equationally; this is the beginning of development with the diploid number of chromosomes (20).

2. One maturation division occurs, without reduction in chromosome number.

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[1] See the discussions by P. Hertwig (1920) and Morgan (1924*f*).

The diploid egg is reported to develop after the formation of a single polar body in a number of cases: *Phylloxera carœcaulis* (Morgan, 1906 etc.), *Aphis saliceti* and *A. palmæ* (de Baehr, 1908–1912, 1920*a*), *Daphnia pulex* (Kühn, 1908), *Miastor* (Kahle, 1908), *Simocephalus vetulus* (Chambers, 1913), *Hydatina senta* in female-producing eggs (Whitney; A. F. Shull, 1921), certain eggs of *Artemia salina* (Brauer, 1894; Petrunkewitsch, 1902; Fries, 1909), the ♀-producing eggs of *Asplanchna* (Tauson, 1924), and two species of *Rhabditis* (Bělař, 1923). In a moth, *Solenobia*, the diploid number in some way becomes doubled, so that the embryo is tetraploid (Seiler, 1923).

3. Two maturation divisions occur, but the egg develops with the diploid number of chromosomes.

In none of the examples in this category have the cytological phenomena been fully cleared up. The most thoroughly examined case is that of *Rhodites rosæ*, a gall-fly (Henking, 1892; Schleip, 1909*b*; Hogben, 1920*a*). Here the 18 chromosomes form nine bivalents, deconjugate, and again associate. Whether haplosis is actually carried out is rendered uncertain by a stage in which the chromosomes form a confused mass; but if it is, the diploid number must be immediately restored by some process not yet understood. Other instances of diploid development after two maturation divisions are found in *Bacillus rossii*, a phasmid (de Baehr, 1907), and *Nematus lacteus*, a saw-fly (Doncaster, 1907).

**False Parthenogenesis.**—The development of an egg without union with a male gamete, but after the fusion of two nuclei. This is called amphimictic parthenogenesis or parthenogamy by Prell.[1]

1. A polar body nucleus fuses with the egg nucleus.

In certain eggs of a phyllopod crustacean, *Artemia salina*, Brauer (1894) reported that the nucleus of the second polar body, with 84 chromosomes, unites with the egg nucleus, causing "fertilization" and the resulting development of a diploid individual. Later workers are doubtful of the interpretation in this case. In *Asterias glacialis* such a behavior was artificially induced by O. Hertwig (1890) and Buchner (1911).

2. The first two cleavage nuclei fuse.

In *Mactra*, a mollusk, after the formation of the two polar bodies has been induced by treatment with salt solutions, the haploid nucleus of the egg divides into two which then fuse, and development proceeds. By proper manipulation of the solutions one or both of the maturation divisions may be suppressed, the oöcyte nucleus then behaving as a cleavage nucleus (Kostanecki, 1911).

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[1] Prell here distinguishes between (*a*) *endomictic parthenogamy:* the fusion of two haploid nuclei from the same diploid clone, as in the union of the egg with the first polar body after prereduction or with the second polar body after postreduction; and (*b*) *automictic parthenogamy:* the fusion of two nuclei from the same haploid clone, as in the union of the egg with the second polar body after prereduction (*Asterias*) or the union of two cleavage nuclei (*Mactra*). We have arbitrarily chosen to use a less refined classification.

**Parthenogenesis and Meiosis.**—The fact that in so many cases parthenogenetic eggs produce but one polar body and remain diploid, while the zygogenetic eggs form two and are haploid, led Weismann and a number of later workers to believe that the second mitosis must effect disjunction in normal meiosis. Although it is now known that disjunction may occur in the second mitosis, the weakness of the argument from parthenogenesis is evident in a consideration of other cases mentioned in the foregoing pages. In the eggs of *Apis* and *Nematus* both maturation divisions take place, with haplosis in the former case but without it in the latter, yet both sorts of eggs develop parthenogenetically. In *Apis*, moreover, haploid eggs develop either parthenogenetically or zygonetically. Recent researches on normal meiosis have shown beyond a doubt that disjunction may occur in either mitosis, even in the same cell (p. 253), although it is probably more often accomplished in the first.

The presence of the leptonema-zygonema-pachynema stages in the prophase of division in parthenogenetic eggs retaining the diploid chromosome number has been taken by some authors to mean that these stages have no significance in connection with haplosis. The untenability of this view is indicated by the phenomena reported for *Aphis palmæ* by de Baehr (1920*a*). Here the eight leptotène threads conjugate parasynaptically and shorten to form four gemini of unlike size. Instead of being distributed by a disjunctional mitosis, the synaptic mates become dissociated within the nucleus, elongate, and split longitudinally. The single mitosis which occurs separates halves of these eight equationally split chromosomes, and the resulting diploid egg develops parthenogenetically. In this case the synaptic pairs which would separate in a normal meiosis are formed in the usual way, but the achromatic mechanism necessary for their distribution for some reason fails to develop. Since the subsequent events proceed as usual, the division in the single mitosis is equational. These phenomena are best explained on the basis of the theory that haplosis normally involves a parasynapsis of leptotène threads and their later mitotic disjunction after shortening. De Baehr interprets the occurrence of the prophasic changes characteristic of the meiotic process in such parthenogenetic diploid eggs as a "phyletic reminiscence" indicating the derivation of parthenogenesis from the usual type of sexual reproduction. In *Artemia salina* (Fries, 1909) the leptotène threads no longer conjugate, but shorten to form the diploid number of chromosomes directly. Just as in plants (p. 356), one may arrange a series of cases in animals illustrating a transition from normal meiosis with sexuality to the absence of meiosis with parthenogenesis, one of the characteristic features of the abnormal cases being a weakness or absence of synaptic attraction between chromosomes in the meiotic prophase. To what extent this abnormal synaptic behavior is due to hybridity in the animals concerned, as it often appears to be in plants, remains to be determined. In the genus *Tephrosia* J. Harrison (1920) observed a case in which the crossing of two non-parthenogenetic species resulted in intermediate hybrids which did produce parthenogenetic eggs. This is distinctly favorable to the theory that there is frequently a rather direct causal relation between hybridization and apomixis.

## CHAPTER XVII

# MENDELISM, MUTATION, AND HYBRIDIZATION

Since the time when a causal relationship between nuclear activity and the phenomena of inheritance was first suggested, the efforts of most cytologists have been devoted directly or indirectly to the solution of two outstanding and closely interrelated problems of biology: the problem of development and the problem of heredity. Although the investigation of many important questions has scarcely begun, cytology has already been able to throw a flood of light upon many previously obscure points involved in both of these major problems.

It should be obvious that the course of any ontogenetic development depends upon the organization of the protoplast with which it begins, *i.e.*, upon the type of protoplasmic system concerned; and also upon the environmental agencies which influence its action. The problem of development is, therefore, to ascertain in what manner intrinsic and extrinsic factors, together composing a single interacting system, operate to produce the succession of changes which constitute ontogenesis; it is a problem pertaining primarily to the individual. But any inquiry of this nature soon leads beyond the individual life cycle to a consideration of the race, and hence to the problem of heredity. The protoplasmic organization upon which the course of development so largely depends is itself an inheritance from the past; indeed, the most fundamental fact which cytology has contributed to the study of heredity is that the protoplasm of successive generations is genetically continuous. These generations pass through the same general series of ontogenetic stages and thus resemble each other for the reason that the protoplasm with which each ontogeny begins is essentially of the same constitution by virtue of this continuity. Generations may be regarded as periodic developments of a persistent protoplasmic system.

It is not solely with resemblances, however, that heredity is concerned. The non-appearance of Mendelian characters in certain generations according to definite rules, and hence the frequent unlikeness of parent and offspring, are known to be just as dependent on the operation of the hereditary mechanism as is their regular appearance in every generation. Even wholly new variations permanently affecting the germinal constitution and so modifying the characters of subsequent generations are supplementary, rather than opposed, to heredity. In the general process of heredity, which involves the effects of variation, we witness the results of processes occurring in a protoplasmic system which, though it maintains a specific type of organization through successive generations, undergoes minor alterations which modify the characteristics of the race. Hence it may be said that *heredity is the occurrence of related conditions or events in successive generations of organisms as a consequence of their protoplasmic organization.*

From these considerations it follows that the problem of heredity which confronts the cytologist is that of ascertaining in what respect resemblances and differences in the characters manifested by successive generations are correlated with similarities and dissimilarities in the organization of the protoplasts with which the successive ontogenies begin, and how such constitutional conditions arise. Search is to be made for a mechanism which remains comparatively stable as it operates through regularly recurring ontogenetic cycles, and yet undergoes orderly alterations of a kind which will help to account for the observed phenomena of heredity and variation, and thus to approach an understanding of evolutionary advance. Heredity, as Thomson (1920) points out, is a condition of evolution, because the persistence of the specific organization is insured by the continuity of the germinal substance; because the emergence of new characteristics is allowed by orderly variations in this organization; and because the specific organization seems clearly to be sheltered from the effects of many somatic modifications which might otherwise prevent any consistent and advantageous series of changes.

**The Rôle of the Nucleus.**—It was Ernst Haeckel (1866) who first advanced the hypothesis that "the nucleus of the cell is the principal organ of inheritance." Cytological evidence in support of this view, announced by Haeckel as a speculation, was brought forward by O. Hertwig (1875, etc.), Strasburger (1878, 1884*a*), van Beneden (1883, etc.), and a number of other investigators, who described the behavior of the nucleus in the various stages of the life cycle, particularly in somatic cell-division, meiosis, and syngamy. Two of these men, O. Hertwig and Strasburger, who had discovered the fusion of the nuclei in syngamy in animals and plants respectively, definitely announced the theory, now supported by a considerable body of observational and experimental evidence, that the nucleus is the "vehicle of heredity." They held that hereditary transmission is through the nuclei of the gametes, and that the chromatic substance is the special inheritance material, or "idioplasm," about which there had been so much speculation. This view was widely adopted by biologists.

The efforts of many cytologists were now directed toward the further elucidation and verification of this nuclear hypothesis of heredity, and many observations and experiments apparently demonstrated its essential correctness. It was noted that, so far as could be discerned, the spermatozoön in many cases brings nothing but nuclear material into the egg, so that hereditary transmission from the male parent must be through the nucleus alone. A similar condition was also reported in certain plants. The male and female gametes, moreover, were seen to differ enormously in volume, yet normally inheritance from the two parents was equivalent. It was only in the nuclei of the gametes that a corresponding structural equivalence could be discovered. Searching investigations of the nucleus and its behavior in division showed that it is composed chiefly of chromosomes, which occur in definite numbers in different kinds of organisms and multiply by division in each mitosis. Furthermore, a large body of evidence led to the conclusion that the chromosomes differ among themselves and in some way maintain an individual continuity through successive generations of cells and organisms. Cytological and genetical researches, which are about to be reviewed, have further made it evident that the relatively stable and specific protoplasmic organization which continues from generation to generation as the material basis of heredity is represented primarily by the nuclear mechanism.

This chapter deals with the orderly changes in this organization which are of special significance in heredity, together with certain apparently less regular phenomena which are known to have decided effects upon the characters of the race. Because of the extensive ramifications of this subject, our treatment must be limited to the most important facts and principles. These may be grouped under the general headings forming the title of the chapter, but it will soon become apparent that they cannot be kept wholly distinct from one another. In Mendelism are seen the results of the distribution of inheritance materials through successive generations; in mutation are seen the effects of quantitative and qualitative alterations in these materials; in hybridization are seen the results of an intermingling of inheritance materials which are unlike. All of these phenomena are intimately related in the study of heredity. Thus Mendelian inheritance is investigated in crosses between unlike types, and crossing is known to be connected with certain kinds of mutation. Although the term "hybridization" often has reference only to the crossing of individuals belonging to fairly distinct varieties or species, the geneticist finds it impracticable to make this arbitrary limitation. The sexual union of any two protoplasms differing in hereditary potency, no matter how slight the difference, constitutes an act of hybridization in the fundamental sense. It is this conception of hybridization that will be borne in mind through the following discussions.

## MENDELISM

The rediscovery in 1900 of the principles of heredity originally announced by Mendel in 1865 marked the beginning of a new era in biology. At once it was shown that the behavior of the chromosomes in the life cycle, elucidated during the closing years of the nineteenth century, parallels in a most remarkable manner the hereditary behavior of the characters studied by Mendel; and since that time cytologists and geneticists have found it necessary to work hand in hand. This significant parallelism will be described in simple and typical examples of Mendelian heredity.[1]

**Typical Cases of Mendelian Heredity.**—Mendel crossed plants of a pure-bred race of tall peas (6 to 7 feet in height) with plants of a pure-bred dwarf race (¾ to 1½ feet in height) (Fig. 170). All the plants of the first filial generation ($F_1$) were tall like one of their parents. When these tall hybrids were self-pollinated [or bred to one another], it was found that the second hybrid generation ($F_2$) comprised individuals of the two grandparental types, tall and dwarf, in the numerical proportion of 3:1. It was further found that the tall individuals of this generation, though alike in visible characters, were unlike in genetic constitution: one-third of them, if bred for another generation, produced nothing but tall offspring, showing that they were "pure" for the character of tallness; whereas the other two-thirds, if similarly bred, produced again in the next generation both tall and dwarf plants in the proportion of 3:1, showing that they were hybrids with respect to tallness and dwarfness. The dwarf plants of the second hybrid generation ($F_2$) produced nothing but dwarfs when interbred; they were "pure" for dwarfness. From these facts it was evident that the plants of the $F_2$ generation, although they formed only two visibly distinct classes, were in reality of three kinds: pure tall individuals, tall hybrids, and pure dwarfs, in the relative numerical proportions of 1:2:1.

The explanation offered by Mendel for these phenomena may be briefly stated as follows. The germ cells produced by the pure tall plant carry something (now termed a *factor*, represented in Fig. 170 by *T*) which makes the resulting plant tall. The germ cells of the dwarf plant carry something (*t*) causing the dwarf condition. In the first hybrid generation ($F_1$) both factors are present, *T* coming from one parent and *t* from the other, but *T* "dominates" and prevents the expression of the

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[1] For detailed accounts of Mendelism, see Morgan *et al.* (1922), Bateson (1913), M. C. Coulter (1923), Castle (1924), Babcock and Clausen (1925), Punnett (1919), Darbishire (1911), Morgan (1919*a*), Thomson (1913), East and Jones (1919), O. Hertwig (1917), Goldschmidt (1920), Baur (1914), Hagedoorn (1921), Walter (1922), D. F. Jones (1925), Wilson (1925). English translations of Mendel's classic paper may be seen in Jour. Roy. Hort. Soc. **26** (1901); also in Bateson's *Mendel's Principles of Heredity* and the first two editions of Castle's *Genetics and Eugenics*. For historical perspective one should read also the work of Naudin, who observed that parental potencies segregate in the germ cells of a hybrid, and that parental types reappear in $F_2$; but who did not show, as Mendel did, that this applies to single pairs of potencies or characters.

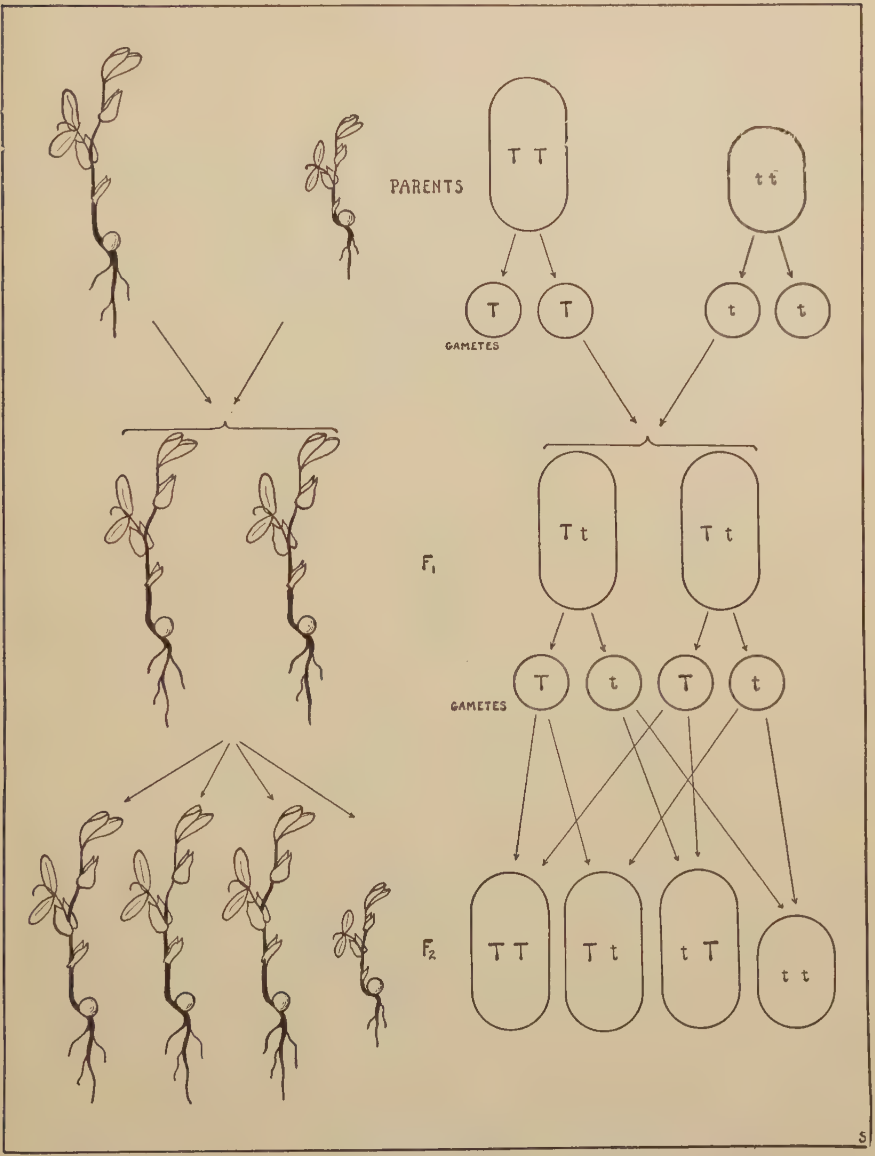

FIG. 170.—A typical example of simple Mendelian heredity. In a cross between pure tall and pure dwarf peas, tallness is dominant over dwarfness in the first filial generation ($F_1$). In the second filial generation ($F_2$) tall plants and dwarfs occur in the ratio 3:1. At the right is shown the distribution of factors for tallness ($T$) and dwarfness ($t$) through these generations. The letters $T$ and $t$ may also be considered as representing a homologous pair of chromosomes.

"recessive" *t*, so that the plants of this generation are all tall. When the hybrid ($F_1$) produces germ cells the two factors for tallness and dwarfness segregate, half of the germ cells receiving *T* and the other half *t*. Each gamete therefore carries either one or the other of the two factors in question, but never both: a given gamete is "pure" either for *T* or for *t*. This segregation in the germ cells of factors previously associated in the individual without their having been altered by this association is the central feature of the entire series of Mendelian phenomena, and is often referred to as *Mendel's first law*. Since the gametes, both male and female, produced by the hybrid plants of the $F_1$ generation are of two kinds (half of them bearing *T* and half bearing *t*), four combinations are now possible: a *T* sperm with a *T* egg, a *T* sperm with a *t* egg, a *t* sperm with a *T* egg, and a *t* sperm with a *t* egg. These four combinations result respectively in a tall plant (pure dominant, *TT*), two tall hybrids (*Tt*), and a dwarf plant (pure recessive, *tt*). It is obvious that in the long run these three types will occur in the ratio of 1:2:1.

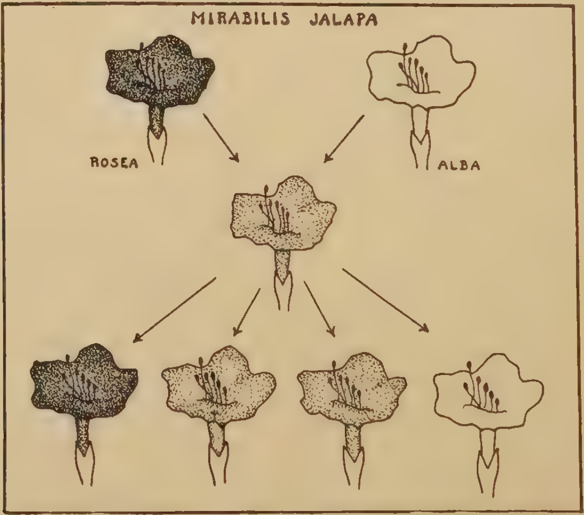

FIG. 171.—Incomplete dominance in *Mirabilis jalapa*. The $F_1$ hybrids are intermediate in character, and in $F_2$ there are 3 phenotypes in the ratio 1:2:1. (*Adapted from Correns.*)

Mendel's researches on peas included also a study of six other pairs of heritable characters (now known as *allelomorphic pairs*), the two members of each pair behaving toward each other in a manner similar to that described above for tallness and dwarfness. He further observed that the seven pairs are entirely independent of each other in inheritance. All these phenomena he interpreted on the basis of the hypothesis that each character is in some way represented by a factor in the cells, new combinations of factors being formed at syngamy and the members of each allelomorphic pair of factors segregating when the germ cells are formed.

The independence of the various pairs of factors formed the basis of *Mendel's second law.* It is now known that many pairs are not thus independent (see p. 469), but the law holds for the seven principal pairs studied by Mendel.

The Mendelian proportion of hybrids and pure forms is better illustrated by characters in which dominance is imperfect or lacking; in fact, complete dominance has been found to be rather exceptional. In such a case as that of *Mirabilis jalapa,* for example, the hybrids are "intermediate," and hence easily distinguishable from the pure parental types (Fig. 171). If plants bearing pure red flowers (var. *rosea*) are crossed with those bearing pure white flowers (var. *alba*) the result is an $F_1$ generation of intermediate pink-flowered plants. When these pink hybrids are bred among themselves the resulting $F_2$ generation comprises plants of three visibly different types: pure dominants with red flowers, hybrids with pink flowers, and pure recessives with white flowers, in the numerical ratio of 1:2:1.

**Terminology.**—We may here introduce certain terms prominent in the literature of genetics. The *genotype* is the entire assemblage of genetic factors, or *genes,* which the organism actually possesses in its constitution, irrespective of how many of these may be expressed in externally visible characters; or it is a class of individuals with the same genetic constitution. The *phenotype* is the aggregate of externally visible characters, irrespective of any other factors, unexpressed in characters, which may be present in the organism; or it is a class of outwardly similar individuals. For illustration: in the case of the tall and dwarf peas there are in the second hybrid generation ($F_2$) three genotypes (with respect now only to the single character pair discussed): *TT*, *Tt*, and *tt*, represented respectively by pure tall plants, tall hybrids, and dwarfs; but there are only two phenotypes: tall and dwarf, because the complete dominance of tallness over dwarfness renders the hybrids externally indistinguishable from the pure tall individuals. Thus one phenotype (tall plants) here includes individuals with two genotypic constitutions, and the two can be distinguished only by a study of their progeny. In *Mirabilis,* however, there are in the $F_2$ generation not only three genotypes represented, but also three phenotypes, since the incomplete dominance renders the hybrids externally unlike either of the pure forms. Practically, a phenotype is a class of individuals which look alike, and a genotype is a class of individuals which breed alike (Castle).

An individual is said to be *homozygous* for a given allelomorphic factor pair if it has received the same factor from the two parents—a pea, for example, with the constitution *TT* or *tt*. If it has both members of the pair, such as *Tt*, it is said to be *heterozygous.* It may be homozygous for some allelomorphic pairs and heterozygous for others, or it may conceivably be either homozygous or heterozygous for all of its factors. Thus an organism with the genotypic constitution *AABbcc* is homozygous for the factors represented by *AA* and *cc*, and heterozygous for those represented by *Bb*. It is thus a pure dominant with respect to *A* and *a*, a pure recessive with respect to *C* and *c*, and a hybrid with respect to *B* and *b*. The phenotypic appearance of the organism would be determined by the dominant factors *A* and *B* and by the recessive *c*. A given dominant factor dominates only its recessive allelomorph, and not the recessive factors belonging to other pairs. It is a common practice to represent dominant factors by capital letters and their respective recessive allelomorphs by the corresponding small letters.

**The Cytological Basis of Mendelian Heredity.**—The history of the chromosomes through the critical stages of the life cycle, as more fully described in the chapters on meiosis and syngamy, must be recalled at this point (see Fig. 172). Each parent furnishes the offspring with a set of individually different chromosomes, the two sets (represented in the diagram by *ABCD* and *abcd*) together constituting the diploid complement present in all of the nuclei of the new individual. When gametes (or spores followed later by gametes in the case of higher plants) are to be formed by this individual, descendants of the homologous chromosomes of the two gametic sets conjugate in pairs (synapsis). In one of the meiotic divisions the two members of each pair disjoin and pass into different nuclei. In the other meiotic division the chromosomes split longitudinally (equationally). The result of the two meiotic divisions, therefore, is a group of four gametes (or spores), two of which differ from the other two with respect to any given chromosome pair: two of them have derivatives of *A* while the others have derivatives of *a*, and so on for all the other pairs.[1] The chromosomes of the diploid complement are in this way assorted into haploid sets, each gamete (or spore) having a set made up of one member of each of the pairs. This set represents the contribution made to the following generation.

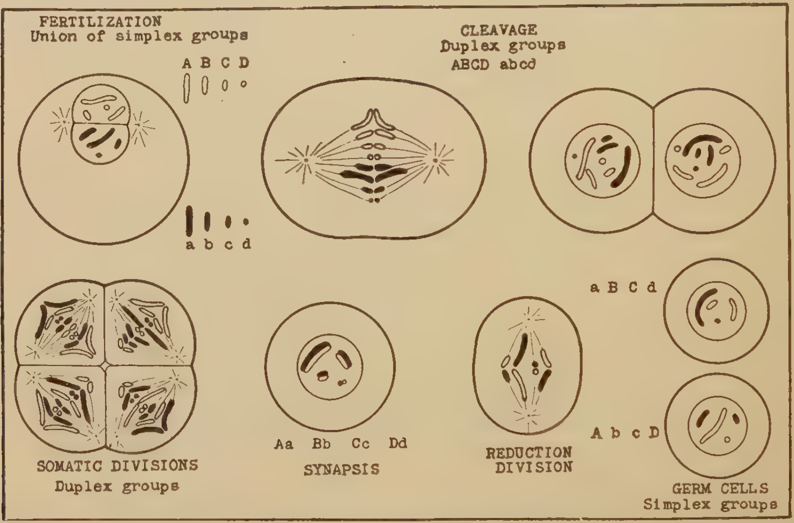

FIG. 172.—Diagram showing the history of the chromosomes in a typical animal life cycle. (*After E. B. Wilson*, 1913.) See also Fig. 103.

It is of importance to note that the various pairs of chromosomes are independent of each other as regards their orientation in the mitotic figure, and hence in their distribution to the daughter nuclei. In some pairs the paternal member is directed toward one pole and in other pairs toward the other pole. It is conceivable that in some cases all the paternal members might go to one pole and all the maternal members to the other. Direct evidence that the assortment of the various chromosome pairs is in this respect a random one, as previously assumed, was furnished by Carothers (1913, 1917). In the grasshopper, *Trimerotropis*, she found that the two members of some of the pairs are visibly different in size, in the mode of attachment to the spindle fibers, and in the presence of constrictions; and that these differences make it possible to show beyond question that the several pairs are entirely independent of one another as regards their orientation in the spindle and their consequent distribution to the daughter nuclei. It has furthermore been shown by the same author (1921) in the case of *Circotettix* that the chromosomes maintain their peculiar forms in subsequent generations, and that all of the possible theoretical chromosome combinations may there be recognized (Fig. 173). Because of the independent distribution of the chromosome pairs in meiosis, a given gamete (or spore) in an organism with four pairs of chromosomes may have any one of 16 possible haploid combinations (Fig. 174).

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[1] It is unnecessary to introduce here the complication caused by chiasmatypy (see p. 284).

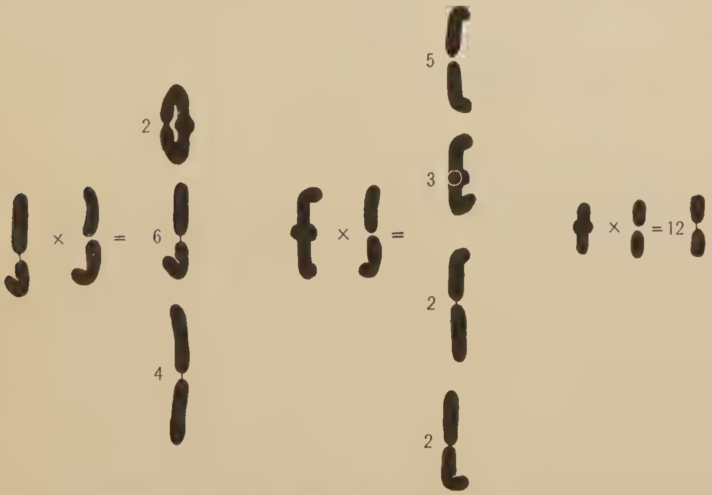

FIG. 173.—Diagram showing the persistence of peculiarities in chromosome form in successive generations of *Circotettix*. When individuals with recognizable peculiarities in a given pair of chromosomes are crossed, this pair in the individuals of the next generation exhibits the peculiarities combined in the various ways theoretically expected. (*After Carothers*, 1921.)

It will be observed at once that the distribution of the chromosomes through the life cycle and successive generations is precisely like that of the Mendelian characters. Two groups of factors for characters are brought together in syngamy and are associated in the body of the offspring. In the germ cells the factors for the two characters forming each allelomorphic pair segregate and pass to different gametes (or spores). The factors and the chromosomes alike form a duplex group in each somatic nucleus and a simplex group in the gametes (or spores): both chromosomes and factors for characters are aggregated in syngamy and segregated in meiosis. The precise nature of the parallelism is seen not only in the factor and chromosome groups as wholes, but also in the individual pairs. If a single pair of chromosomes, for example *Aa* in Fig. 172, be followed through successive cycles it will be seen that *there is an exact parallelism between the distribution of a given homologous pair of chromosomes and that of a single allelomorphic pair of Mendelian factors.* This is just the condition that should result if the two factors are present as units of some kind in the two members of the pair of chromosomes. In the disjunction of these members in meiosis is recognized a cytological mechanism adequate to accomplish the factorial segregation underlying Mendel's first law. In Fig. 170 the symbols *T* and *t* may be taken to represent either a pair of factors or a pair of chromosomes. Moreover, a basis for Mendel's second law is seen in the independent distribution of the various chromosome pairs. Different factor pairs are independently distributed, as Mendel held, if they are associated with different chromosome pairs; but this will not be the case if they lie in the same pair. The discovery of "linkage" has accordingly made necessary an important qualification of Mendel's second law, and this has served to show even

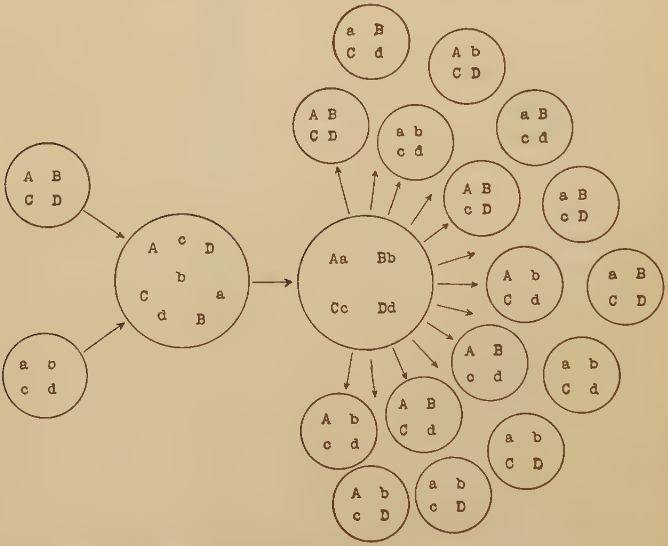

FIG. 174.—Diagram showing the 16 genotypic combinations which may characterize the gametes of an organism with only 4 independent heterozygous pairs of factors. (*After E. B. Wilson*, 1913).

more strikingly than before the unquestionably significant relation between Mendelian heredity and chromosome behavior (Chapter XX).

**The Factorial Hypothesis.**—The parallelism between the behavior of the chromosomes and that of Mendelian factors led to the definite formulation of the hypothesis that the factors are actually material units, or *genes*, located in the chromosomes, each allelomorphic pair of genes being assigned to some one homologous pair of chromosomes. For the sake of simplicity a character is often treated as if it were due to a single gene or "determiner," but this is far from what is actually assumed in the factorial hypothesis. In the words of Bridges (1923):

> . . . the genes of the entire complement act together, since all are liberating their chemical products into the common cytoplasm. But since the products of the different genes are different they take effect in different ways upon the developing organism. Thus some of the genes will have much effect upon one character but little effect upon another. Each character will be determined by all the genes, but in each case most of the effect will be produced by a much more limited number. Each particular character shows a grade of development corresponding to the number and effectiveness of the genes that are producing it. In the case of many of the characters there are genes tending to make the character less pronounced, and the grade realized is that corresponding to the equilibrium between these plus and minus modifiers. The directions of modification for each character are in general quite diverse, and it is somewhat for the sake of simplicity that they are lumped together as plus and minus modifiers.

These facts, however, do not preclude the convenient practice of singling out the most conspicuous effect of a gene, or the most influential gene or genes in the case of any particular character, though in so doing one may use expressions which are easily misunderstood. "The factorial hypothesis does not assume that any one factor produces a character directly and by itself, but only that a character in one organism may differ from a character in another because the sets of factors in the two organisms have one difference" (Morgan *et al.*, 1915). Hence the introduction of a new gene is not actually the introduction of a new character, but rather the addition of an element which may alter the total action of the gene system and so affect its results, which may be most pronounced in one character. The action of a gene depends largely upon the nature of the system of which it is a part; in one combination its principal effect may be different from that in another.

The Mendelian results are greatly complicated by a number of phenomena, such as the presence of more than one gene with similar pronounced effects (multiple factors; blending inheritance); the presence of "lethal factors," which in certain combinations destroy the organism; the frequent differential vigor of gametes with different genic combinations; and a number of other conditions which the geneticist must take into account. In spite of the complexity of such results, they seem to show fundamental agreement with the simple cases described above, which are sufficient to show the bearing of cytology on the study of Mendelian heredity.

The expression "factorial hypothesis" usually has reference to the conception of Mendelian factors or genes, but it should be obvious that any comprehensive interpretation of organic phenomena in terms of contributory causes must include the action of other factors as well. It is to be strongly emphasized that the system in which the phenomena of heredity and development occur is the *organism-environment.* There is probably no character which can be attributed solely to the organism or to the environment; these two components of the system it appears impossible to separate in any real sense. What an organism inherits is not a set of characters, but a number of capacities to react in certain ways under certain conditions, the developed characters being the result of the action of the entire system of which the organism and environment are integral parts. The relative differential effects of genetic and non-genetic factors may be expected to vary under appropriately varying circumstances.[1]

**Mendelism in Haplonts.**—The principles enunciated by Mendel were based on phenomena observed in *diplonts,* or organisms with diploid somatic nuclei and haploid gametes. Since that time most genetic investigations have been carried on with such organisms. It will now be of interest to see whether or not the same principles hold in the case of *haplonts,* that is, organisms having the haploid number of chromosomes in their somatic nuclei.

The chromosome cycle of a typical green alga is shown in Fig. 175. The haploid individuals produce haploid gametes which fuse to form a diploid zygote (oöspore or zygospore). The chromosome number is immediately reduced when the zygote germinates, the haploid products of meiosis (here represented as spores) giving rise to the haploid individuals of the next generation. The cycle is the same in the bryophytes, except that the zygote germinates to form a diploid sporophyte in which meiosis is delayed until sporogenesis. In the body of an alga or a moss gametophyte, therefore, only one member of each homologous chromosome pair is present in each nucleus, rather than both of them as in diplonts.

The expectations based on the chromosome theory of Mendelism are as follows: Two contrasting "allelomorphic" characters of the gametophyte introduced into a zygote by crossing should segregate at once in the next gametophyte generation in the ratio of 1:1. In the haplont, therefore, there should be no "dominance," since only one factor of a given pair is present; hence the appearance of a character of one parent to the exclusion of the allelomorphic character of the other cannot mean that the factor for the latter may be present but obscured by the formed Any factor, whether more or less potent than its allelomorph, should produce its full effect in the next generation; phenotype and genotype are here in correspondence. The outward resemblance of an individual to its two parents should, therefore, be determined simply by the relative number of factors received from each of them. In diplonts the number of factors received from the two parents is the same, resemblance to the parents depending on the relative number of *dominant* factors contributed by them. In diplonts there is one genotype in $F_1$ and three in

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[1] For discussions of this point, see Emerson (1924), Jennings (1924), Sharp (1925).

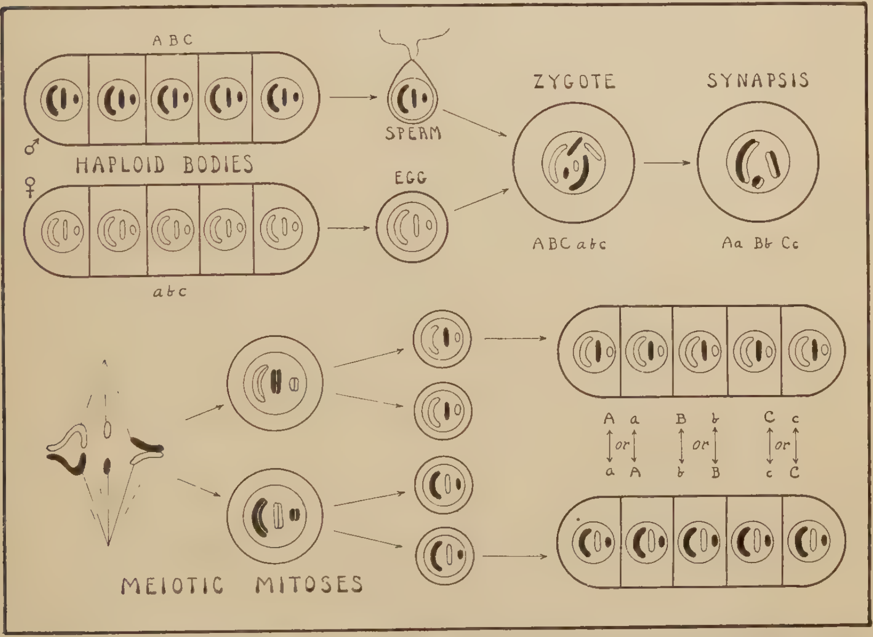

FIG. 175.—Diagram illustrating the behavior of the chromosomes through the life cycle of a haplont. Owing to the independent orientation of the several chromosome pairs in the meiotic mitoses, a given haploid individual may have any one of 8 possible chromosome assortments (when there are 3 pairs of chromosomes).

$F_2$ (with respect to a single allelomorphic pair), but in haplonts there should be two in every generation. Two character pairs should give four genotypes in the haplont offspring and three pairs should give eight. In the following cases it will be seen that these expectations are realized.

In the moss genera *Funaria* and *Physcomitrium* von Wettstein (1921*b*, 1923, 1924) studied the progeny of crosses between types differing in various pairs of contrasting gametophytic characters, and found that such characters segregate 1:1 in the next generation. For example, when two types differing in leaf form were crossed, the spores from the hybrid capsule produced gametophytes of the two parental types in equal numbers. The size of the spore itself is such a gametophytic character.

The sporophytic characters (form and color of capsule) were inherited as would be expected in diplonts. Von Wettstein was able to show that the segregation of the factors for the gametophytic characters takes place in each sporocyte: two spores of a quartet produce one type of gametophyte and two produce the other. This clearly indicates a segregation in one of the meiotic divisions.

In the liverwort, *Sphærocarpos Donnellii*, C. E. Allen (1924*ab*, 1925*a*) has shown that the gametophytic character "polycladous" segregates from its allelomorph "typical" nearly 1:1 in the first gametophyte generation after a cross, and that two spores of a quartet produce one type and two the other. The same holds for the character "tufted." Both characters are independent of sex, which had formerly been shown to be inherited in the same manner (p. 428). Hence the spores produced by a single hybrid sporophyte give rise, for example, to tufted males, tufted females, typical males, and typical females. Ordinarily the spores of a single quartet are of only two of these types. But Allen found a few exceptional cases in which all four were present; whether this should be attributed to an occasional disjunction of two chromosome pairs in different meiotic mitoses or to some other cause, perhaps chiasmatypy, cannot at present be stated. With regard to sporophytic characters, Allen (1925*b*) has shown that the tendency to mature the spores separately or united in quartets is transmitted through the female gametophytes only. Hence there is here a sex-linked character pair, the distribution of which parallels that of the $X$-chromosome.

Another problematic case is reported by Pascher (1916). Two species of *Chlamydomonas* differing in certain characters of the swimming cell and of the zygote were allowed to conjugate. The hybrid zygote showed a combination of the parental zygotic characters, as would be expected. Of the four swarmers arising from this zygote, two were found to be of one parental type and two of the other, in five of the cultures. In three cultures, on the other hand, the four swarmers were of four intermediate types. The time of meiosis in *Chlamydomonas* is not certainly known, but it is presumed to occur in the germination of the zygote.

In *Spirogyra* three of the four nuclei formed at meiosis degenerate. If all of the four nuclei have an equal chance of survival, statistical study should show how the factors are segregated in meiosis. Such a study has been made by Transeau (1919). Hybrids between various species are of the two parental types in equal numbers, so far as any one pair of characters is concerned. When two pairs of characters are considered, the hybrids are of four types, and when three are considered, they are of eight types. These results are in accord with the expectations based on the independent assortment of factors and the equal chance of survival of the four meiotic nuclei. It is of interest to note that the form of the zygospore in *Spirogyra* behaves as a maternal character.

The inheritance of simple characters in pollen grains of angiosperms has been investigated in connection with this problem. Since the pollen cells belong to the haploid phase of the life cycle, the offspring of two parents differing in pollen characters should produce pollen of the two parental types in equal ratio if such characters are due solely to the factors in the haploid nuclei. This has been found to occur.[1] In *Stizolobium* Belling (1914, 1915) observed the abortion of 50 per cent of the grains, which also indicates a segregation of factors in meiosis. Contrasted with these cases are certain others[2] in which the pollen characters (chiefly color and shape) show dominance and behave as sporophytic characters, which is not surprising in view of the fact that the grains are developed in the midst of diploid sporophytic cells (tapetum, etc.) and are known to make use of materials derived from them. Pollen may therefore exhibit "sporophytic" as well as "gametophytic" characters, owing to the intimate association of the two phases of the life cycle.

The results of experiments on haplonts afford very definite corroboration of the chromosome theory of Mendelian heredity originally propounded on the basis of studies on diplonts. Further evidence is found in organisms with more than the diploid number of chromosomes.

**Further Corroborative Evidence.**—The endosperm of anigosperms is triploid: each nucleus contains one haploid set of chromosomes from the father and two from the mother; in ordinary cases the latter two are qualitatively similar. Hence endosperm characters should show a form of inheritance determined by the presence of two factors of each kind from one parent to one from the other. This has been found to be the case. In some instances, however, the results are complicated by the fact that dominance may depend on which of the two allelomorphic factors is present in duplicate, the character of the endosperm thus being like that of the maternal parent (East and Hayes, 1915, on *Zea*). The effect of the pollen parent on the endosperm (*xenia*) is thus obscured in the case of certain characters. A similar "reversal of dominance" has been reported by von Wettstein (1923) in triploid moss plants.

Very striking additional evidence for the chromosome theory is found in triploid and tetraploid angiosperms. In a tetraploid *Datura stramonium*,[3] for example, the homologous chromosomes are present in groups of four (tetrasomes) rather than in pairs (disomes), and the inheritance of the characters concerned is such as would follow a random distribution of the four chromosomes in meiosis. In the same way the inheritance in triploid plants, produced by crossing diploids with tetraploids, is in accord with a random distribution of the members of the trisome. The peculiar genetic ratios so far observed in polyploid plants are what would be expected on the basis of the chromosome distribution.

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[1] *Œnothera* (Renner, 1919*ab*); *Oryza* (Parnell, 1921); *Zea* (Demerec, 1924; Brink and MacGillivray, 1924; Longley, 1925).

[2] *Epilobium*, *Papaver*, and *Geranium* (Correns, 1900, 1902); *Lathyrus* (Bateson, Saunders, and Punnett, 1905); *Nicotiana* (Thomas, 1913).

[3] Blakeslee (1921–1924), Blakeslee and Belling (1924), Belling and Blakeslee (1922, 1924*ab*), Blakeslee, Belling, and Farnham (1923), Blakeslee and Farnham (1923).

Mention may also be made of the fact that organisms reproducing asexually with no meiosis show no Mendelian segregation and a notable genetic stability. Thus Agar (1920*b*) observes in *Daphnia* that individuals developing from parthenogenetic eggs produced by a hybrid without chromosome disjunction show no evidence of a segregation of factors. Abnormal chromosome behavior in all such cases is accomplished by corresponding abnormalities in Mendelian heredity.

**The Bearing of Mendelism on the Problem of the Origin of New Types.**—This subject can be more profitably discussed after having dealt with the further topics of this chapter, but it will be well to point out here the abundant opportunity for the formation of new factor combinations through crossing. Inspection of Fig. 174 will show that an organism with four heterozygous and independent pairs of genes may form as many as 16 types of gametes with respect to these genes. If such an organism is self-fertilized (or if two similar ones are crossed) there may arise as many as 81 different combinations in the offspring. Further crosses with other types will, of course, give many more combinations.

In such a way one may calculate the number of combinations possible among the numerous genes actually present. As will be explained in a later chapter, the genes are not all independent, but are transmitted in groups, each chromosome carrying a considerable number of them. It can readily be calculated that 12 unlike pairs of chromosomes, with the members of each pair showing some degree of heterozygosity, may form 4,096 ($=2^{12}$) different haploid combinations in the gametes, and 16,777,216 ($=3^{12}$) diploid combinations in the next generation after self-fertilization; *i.e.*, this is the number of possible combinations of genic groups. If two such individuals differing in all their chromosomes are crossed, there will be $4^{12}$ possible kinds of genotypes in $F_1$ and $10^{12}$ in $F_2$ and subsequent generations (see Winge, 1919*b*). The number of gene combinations will be still greater if there is an interchange between the groups through chiasmatypy. Whether or not chiasmatypy is the mechanism concerned, there is abundant evidence that such a "crossing-over" between groups of genes takes place (see Chapter XX).

The production of even these enormous numbers of recombinations of Mendelian factors would of itself seem to be of limited influence in furnishing the basis for evolutionary advance. Repeated shuffling of the same lot of genes would lead to great diversity, but to little that is actually new unless the genes themselves undergo some change. This leads directly to the subject of mutation.

## MUTATION NOT INVOLVING CHANGE IN CHROMOSOME NUMBER

The term *mutation* may be used in a general sense for all types of alteration in the hereditary substance aside from that accomplished by normal meiosis and syngamy, the types being classified on the basis of the amount of the substance involved (gene; group of genes or section of chromosome; chromosome; chromosome set), and the nature of the process causing the alteration (Bridges, 1923). There is a tendency among some geneticists, however, to restrict the term to gene mutations.

**Gene Mutations.**—The hypothesis that the comparatively stable gene may under certain occasional circumstances undergo a qualitative change with an effect upon one or more characters underlies much of the genetic investigation now in progress. It is supposed that such an alteration may involve a single locus or gene ("point mutation") or a group of linked genes occupying a certain region of a chromosome ("regional mutation" or "complex mutation"). There is genetic evidence to show that gene mutations may occur at any place in the organism or stage of the life cycle, but they are most frequent in the germ cells at or near the meiotic period.[1] Ordinarily, therefore, only a few of the many reproductive cells transmit the altered gene. If, as seems to be true of the majority of known cases, the mutation is from a dominant to a recessive condition, the effect on the characters of the diploid organism will not be fully manifested until two such recessive allelomorphic genes are brought together.

Gene mutations occurring in body cells are known as *somatic mutations*. Two of the most conspicuous results of somatic mutation in plants are bud sports and chimeras. If the mutation occurs in the meristematic tissue of a very young bud, the entire product of the bud—branch, flower, or flower cluster—has a new genotypic constitution and exhibits an appearance often strikingly different from that of the other branches or flowers of the plant; hence the term "bud sport." Such a mutation occurring in a partially developed shoot or organ may result in a chimera, in which a distinct portion of the mature structure, commonly a sharply defined sector, differs constitutionally and in appearance from the other portions. Analogous changes occur in animals. Somatic mutations in the young pistillate inflorescence of maize result in colored areas of a size depending on the stage at which the change occurs. If it takes place at an early stage of development, the area may include a large portion of the cob and many kernels; if it occurs late there are only smaller spots on the kernels. Calculations have shown that these mutations occur with increasing frequency as maturity is approached, and that the increase is far greater than can be accounted for on the basis of the increased number of cells in which mutation might take place.

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[1] Emerson (1914, 1917, 1922), Eyster (1924), Bridges (1919), Muller (1920), Blakeslee (1921), E. G. Anderson.

Such mutational changes are inherited only if they take place in the lineage of the reproductive cells. Many occur after the latter cells have been differentiated, or in parts of the plant which produce no such cells. Some pericarp mutations in maize which are not inherited are supposed to take place in the epidermis, which is developmentally distinct from the inner tissue in which the reproductive cells arise (Emerson). Likewise in *Datura* certain new characters manifested in the altered color of petals but not transmitted through the seeds are attributed to epidermal mutations. Similar mutations occurring in subepidermal tissue and not at once affecting the petals may be revealed in the petals of the next generation, since all the tissues of the plant, no matter how distinct from one another they may be during the later developmental stages, arise from the same zygote.

By some geneticists somatic mutations have been thought to be due to the segregation of two heterozygous allelomorphic genes in vegetative divisions; the recessive gene, thus freed from the dominance of its allelomorph, is then able to produce its characteristic effect upon the tissues. This explanation appears plausible in the case of recessive mutations, especially since a non-separation of daughter chromosomes has occasionally been observed in somatic tissues; but it will hardly account for mutations from the recessive to the dominant condition, which have frequently been observed (*e.g.*, in maize pericarp by Emerson, and in the elytra of *Bruchus* by Breitenbecher, 1922). The hypothesis of gene mutation is in better accord with the sum of the evidence.

The nature of the mutational change which may thus occur in the gene is unknown, since the nature of the gene itself is almost wholly a matter of conjecture. The literature of genetics contains many interesting speculations on this subject, various comparisons with molecules, radicals, colloidal aggregates, and enzymes being suggested. Whatever its nature, the gene appears to have a high degree of stability, and is not easily influenced. So far almost nothing is known about the causes of gene mutation, although the effects of temperature (Krafka on *Drosophila*, 1920) and anti-lens serum (Guyer and Smith on rabbits, 1918, 1920) appear to be of considerable significance in this connection. The stimuli to which the genes respond by undergoing some constitutional change are probably for the most part internal ones. Although the number of ways in which a gene may change is limited by its own organization, the possible changes are nevertheless numerous; and it is very probable that a large share of the variations which constitute initial steps in evolution originate in this manner.[1]

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[1] See Conklin (1919–1920), Muller (1922, 1923), Muller and Altenburg (1919), Morgan (1922), Goodrich (1921), Castle (1923), Hagedoorn (1921), Gates (1915, 1920*b*).

**Balanced Lethals.**—It appears that some genes in certain combinations may prevent development and thus bring about the death of the organism; they are lethal factors. In races with such factors present, some of the expected classes do not appear in the progeny after certain crosses, owing to the early death of certain individuals. Thus an organism of hybrid constitution may breed true, owing to the non-development of the homozygotes, if the lethal factors produce their effect only when present in duplicate. Muller (1917, 1918) thus explained certain genetic behavior in *Drosophila* and *Œnothera* on the basis of a theory of "balanced lethals." To many geneticists this theory appears to clear up the much discussed problem of *Œnothera* (Morgan *et al.*, 1922; G. H. Shull, 1923, Davis, 1923), but there is some question regarding the evidence in this case (S. H. Emerson, 1924). In the words of B. M. Davis (see Fig. 176):

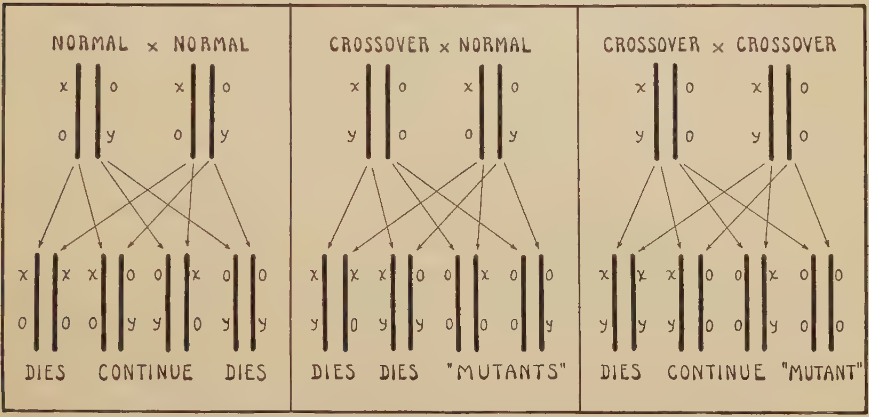

FIG. 176.—Diagram illustrating the theory of balanced lethal factors. Explanation in text.

> The theory of balanced lethals postulates the presence of two different lethals, for example $x$ and $y$, the first in one chromosome and the second in the other chromosome of a synaptic pair [but not at corresponding loci]. The organism is therefore heterozygous for each lethal. The theory also assumes that each lethal is effective only in double dose. The reduction divisions in such material will give two classes of sperms and two classes of eggs, each class distinguished by the presence of one of the two lethals. Thus there will be sperms $x$ and $y$ and eggs $x$ and $y$ and the chance mating of these will give zygotes in the following proportions $1xx:2xy:1yy$. Zygotes $xx$ and $yy$, because they have lethals in double dose, cannot develop progeny, but the zygotes with the heterozygous combination $xy$ will live and reproduce the impure or hybrid parent type. Thus an impure species or race will breed true and maintain a constant state of hybridism unless the relative position of the lethals is changed by a crossover or unless a lethal becomes ineffective through a mutation. A crossover makes possible a class of

zygotes free from both lethals, because sperms and eggs would be of the two classes *xy* and *oo* and the zygotes would be in the proportions 1*xxyy*: 2*xy*: 1*oo*. Through the class of segregates free from both lethals, recessive characters would appear if genes responsible for their suppression were removed by way of the class homozygous for both lethals. The appearance of such recessives will simulate mutations although in reality they are manifestations of a process of segregation.

In addition to such "zygotic lethals" geneticists have been led to postulate "gametic lethals" which in a similar manner prevent the formation of certain expected classes of gametes. Hence if there are factors which in certain combinations are unfavorable to the development of the gamete or embryo, many aberrant genetic ratios may receive explanation.

**Cytoplasmic Mutations.**—Under the head of mutational changes not involving changes in chromosome number may be included those little-understood cases of alteration of cytoplasmic constitution which show themselves in the plastids (p. 417). It is only in a broad sense that these can be called "mutations." Reference has been made to the uncertainty regarding the rôle of the nucleus in such cases, and at present it seems best not to confuse them with mutations clearly involving the chromosome mechanism.

**Chromosome Aberrations Not Affecting Number.**—Mention may also be made here of certain mutants whose chromosome complements comprise normal numbers but abnormal assortments. Thus in certain aberrant types of wheat Winge (1924) observes that the chromosomes are present in the normal number, but include a trisome or tetrasome along with the paired members. This is taken to mean that one or more chromosomes have been lost through non-disjunction and replaced by others not homologous with them, the genic complex and hence the external appearance being altered. Similarly, in tetraploid *Daturæ* Blakeslee and Belling have found a modified type in which a lack of one chromosome is offset by an additional chromosome of another kind; the number of chromosomes is normal $(48 - 1 + 1 = 48)$, but the make-up of the complement is abnormal.

Such cases serve admirably to illustrate the important point that chromosome number, although it affords a convenient basis for classifying the many types of mutants, is not the feature upon which attention should be centered. The fact of prime significance is that chromosomal aberrations with an influence on the organism's characters involve *qualitative alterations in the genic system.* Such changes can frequently be detected in comparisons of the size, shape, and arrangement of the chromosomes of the complements in question. Although numerical differences, when present, are important, it is obvious that chromosome complements may vary widely in constitution irrespective of such easily observable differences.

## MUTANTS AND HYBRIDS WITH CHANGED CHROMOSOME NUMBER

New types appearing spontaneously with altered chromosome numbers are usually referred to as mutants. Since, however, they in many cases exhibit chromosomal aberrations like those observed in hybrids, and frequently show many of the other characteristics of hybrids, such mutation and hybridization are doubtless very closely related phenomena. They may therefore be treated together.

**Polyploidy.**—Polyploid forms are those possessing more than two complete homologous sets of chromosomes in the nucleus. When the total number is thus an exact multiple of the fundamental haploid number the term *euploid* (Täckholm, 1920) may be employed.

*Tetraploids.*—In a tetraploid individual there are four chromosomes of each kind, rather than two as in a diploid. For some time the best-known examples of tetraploidy were the *gigas* mutants of *Œnothera*, with 28 chromosomes instead of 14 in their somatic nuclei (Fig. 177). Tetraploid species or varieties are now known in many genera. Typical examples are *Primula Kewensis*, with 36 chromosomes instead of 18 (Digby, 1912; Dahlgren, 1916), several species and hybrids of *Rosa*, with 28 instead of 14 (Täckholm, 1920, 1922; Blackburn and Harrison, 1921; Penland, 1923), and *Datura*, with 48 instead of 24 (Blakeslee, *et al.*).

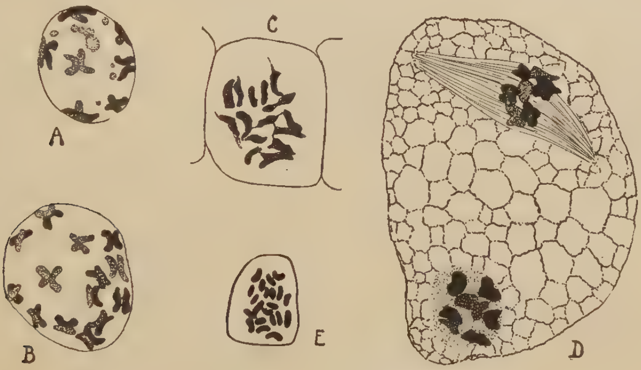

FIG. 177.—Chromosomes in *Œnothera* mutants.

*A*, interkinesis in *Œ. Lamarckiana;* 7 split chromosomes. *B*, same in *Œ. gigas;* 14 split chromosomes. *C*, somatic cell of *Œ. semilata;* 15 chromosomes. *D*, metaphase of second meiotic mitosis in *Œ. biennis lata*, showing 8 chromosomes in one figure and 7 in the other; spores and gametes with these numbers will result. *E*, the 21 chromosomes in a mutant from *Œ. Lamarckiana.* (*A and B after Davis*, 1911; *C and D after Gates and Thomas*, 1914; *E after Lutz*, 1912.)

Tetraploid mutants are frequently characterized by an unusually large size, not only in the plant as a whole but also in its anatomical constituents (Winkler on *Solanum*, 1916; Tupper and Bartlett on *Œnothera stenomeres*, 1916). This, however, is not always true. Moreover, not all cases of gigantism are associated with tetraploidy: in a form of *Primula sinensis* (Gregory, 1909, 1914) and in *Phragmites communis* (Tischler,

1918) it is associated with an increase in the size of the chromosomes but not of their number. Sinotô (1925) reports that in *Plantago japonica*, a giant form, the number of chromosomes (12) is only one-half that in the ordinary *P. major*, var. *asiatica*. Although the volume of the nucleus is less in *japonica*, the cell size is about the same in the two species; the cells are accordingly more numerous in the larger species. It has been suggested by Blakeslee, Belling, and Farnham (1923), as a result of their studies on *Datura*, that in tetraploids with four homologous chromosomes assorting at random, a change may occur whereby they behave as two regular pairs (the "double diploid" condition); or even that the like chromosomes conceivably may fuse in pairs, giving the diploid number of larger chromosomes, as in *Primula*. Only future research can show whether or not such changes actually occur, and what effect they may have upon the expressed characters.

*Triploids*.—Triploid species, varieties, or forms are, like tetraploids, of fairly common occurrence among plants, and they are also known among animals. The *Œnothera* mutants of the *semigigas* group have 21 chromosomes instead of the diploid 14. Triploid roses also have 21. Triploidy occurs occasionally in *Drosophila*, and has led to significant results in the study of sex and other characters (Bridges). The interesting cytological behavior in forms with an odd number of chromosome sets will be discussed later.

*Other Multiples*.—In addition to the foregoing categories, there are found many examples of higher multiples of the basic haploid number. In the genus *Rosa*, for example, pentaploid, hexaploid, and octoploid forms are known, as well as diploids, triploids, and tetraploids (Täckholm, 1922). Decaploids are known in *Chrysanthemum* (90 chromosomes; Tahara, 1915*b*, 1921) and in *Papaver* (70 chromosomes; Ljungdahl, 1922). In *Senecio*, which has 5 as its basic number, Afzelius (1924) reports one species with about 90 chromosomes.

It is a very significant fact that a considerable series of multiples may occur within a single family or genus. In *Chrysanthemum*, for example, there are species with 9, 18, 27, 36, and 45 pairs of chromosomes. In a large number of species of *Senecio* and related genera the numbers are nearly all multiples of 5 (Afzelius, 1924). Mention has been made of the similar series in *Rosa*, in which the basic number is 7 (Fig. 178). In *Triticum* the diploid numbers are 14 (Einkorn group), 28 (Emmer group), and 42 (Spelta group) (Sakamura, 1918; Kihara, 1919; Sax, 1921, 1922) (Fig. 185). In the Compositæ three series of genera may be distinguished with basic numbers of 4, 5, and 9 respectively (Rosenberg, 1917). Many other similar cases might be cited.

The bearing of such "euploid series" or "orthoploid series" on the problem of the differentiation of species and varieties will be discussed later. It may here be observed that species groupings made on the basis of chromosome number frequently correspond strikingly with those arranged by taxonomists on other grounds. A good example is seen in the genus *Triticum.*[1]

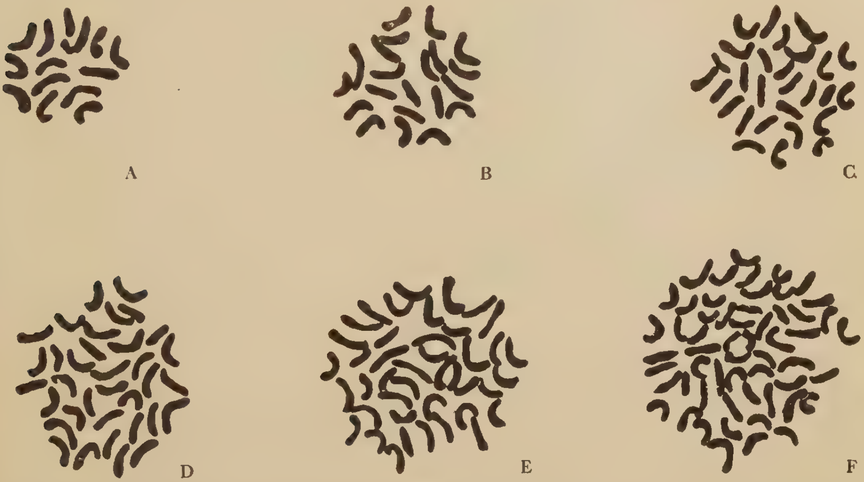

FIG. 178.—The diploid chromosome complements of various species of *Rosa*, illustrating euploidy. *A*, *R. webbiana*, 14 chromosomes. *B*, *R. chinensis*, 21. *C*. "Konrad Ferdinand Meyer," 28. *D*, *R. tomentosa cuspidatoides*, 35. *E*, *R. nutkana*, 42. *F*, an octoploid hybrid, 56. (*After Täckholm*, 1922.)

*Haploids.*—Haploid mutants, though obviously not polyploid, may be mentioned here. The appearance of haploid individuals among organisms normally diploid is a very rare occurrence. It has already been pointed out how frequently such organisms show a peculiar inability to proceed very far in development with only one set of chromosomes (p. 360). In *Datura stramonium* Blakeslee and his associates (1922) discovered the first known case of a haploid angiosperm sporophyte. Several such plants have now been obtained by these workers. They are somewhat weaker than normal diploids, but grow successfully to sexual maturity. Clausen and Mann (1924) report the discovery of two haploid plants among their *Nicotiana tabacum* hybrids.

**Aneuploidy.**—Aneuploid forms (Täckholm, 1922) are those having somewhat more or somewhat less than a euploid (usually the diploid) number of chromosomes, but not a multiple of the basic haploid number. It is of interest that such forms usually differ in appearance from the normal diploid much more than do the tetraploids, triploids, or other euploid forms. Apparently there is a "balance" within the complement which is maintained even when three, four, five, or more haploid sets are present, but which is disturbed when any set lacks one or more chromosomes or has them present in excess. Such disturbances in the normal ratio of inheritance elements caused by the addition or loss of chromosomes or sections of chromosomes are called "ratio mutations" by Bridges (1923). Aneuploids with extra chromosomes ("hyperploids," Winkler) are of common occurrence, but the corresponding "hypoploids" are comparatively rare; the loss of a chromosome seems to cause a more serious "unbalance" than does the gain of one. The best-known aneuploids are those with one more than the diploid number—the $2n + 1$ forms, exemplified by *Œnothera lata* and certain *Datura* mutants.

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[1] Schulz (1913), Zade (1914, 1918), Sakamura (1918), Kihara (1919, 1921, 1924), Sax (1921, 1922, 1923), de Mol (1924).

In the *Œnothera* mutants of the *lata* group there are 15 chromosomes rather than the normal 14; one of the chromosomes is present in triplicate while the rest are in duplicate as usual[1] (Fig. 177, *C*). Lutz found mutants of several types in this 15-chromosome group, which suggested that the chromosome present in triplicate was not always the same member of the complement. In *Œ. scintillans* Hance (1918) was able to distinguish the extra chromosome by measurement.

The mutants of *Datura stramonium*, investigated by Blakeslee, Belling, and their associates, represent the most fully analyzed cases of aneuploidy in plants. In *Datura* the haploid set consists of twelve chromosomes: one very large, four large, three large medium, two small medium, one small, and one very small. Haploid mutants have one such set, normal diploids have two, triploids have three, and tetraploids have four. In addition to these euploids, a considerable series of $2n + 1$ mutants has been found; and it is noteworthy that the number of primary types of such mutants is 12. Since this is the basic chromosome number, each of the 12 primary types would seem to be due to the presence in triplicate of a particular one of the 12 chromosomes, and there is much genetic and cytological evidence to show that this is actually the case. Such $2n + 1$ forms are called "simple trisomic" mutants; they have 11 disomes (normal pairs) and one trisome. Other modified diploids are also known: "double trisomic" forms have two of the chromosomes in triplicate ($2n + 1 + 1$); "simple tetrasomic" forms have one of the chromosomes in quadruplicate ($2n + 2$); and so on. Modified tetraploids and triploids are also known. A $4n + 1$ form is called a simple pentasomic, and a $4n - 1$ a simple trisomic type.

The unbalancing effect of extra chromosomes is well illustrated in the "globe" mutants, which are due to an excess of a certain one of the 12 chromosomes. It is found that the $2n + 2$ globe has the characteristics of this mutant more accentuated than the $2n + 1$ globe, and the same is true of the $4n + 2$ as compared with the $4n + 1$ forms; in each case the degree of nuclear unbalance is reflected in the somatic appearance. It has furthermore been found that the 12 primary $2n + 1$ mutants differ not only in their external appearance, but also very characteristically in the details of their anatomical structure (Sinnott and Blakeslee, 1922). Under each primary type various secondary types may be recognized; these seem to be due to different arrangements of the elements of the trisome. Blakeslee and Belling (1924*b*) have recently reported several "chromosomal chimeras," in which single branches on diploid plants show $2n - 1$, $2n + 1$, or $4n$ chromosomes. It also seems probable that epidermal and subepidermal tissues may sometimes differ in the same manner.

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[1] Lutz (1912, 1917), Gates (1912), Gates and Thomas (1914).

As in the case of euploid numbers, aneuploid numbers seen to arise in mutants are found also in the varieties or species of certain taxonomic groups.

### CHROMOSOMES AND SPECIES ALTERATION

The discovery of the relative uniformity of the number of chromosomes in an individual or species led to the determination of the number in many organisms belonging to all of the major groups. A certain amount of speculation regarding the general phylogenetic significance of chromosome number has been indulged in, but students of the subject have reached the conclusion that the data at hand do not warrant many broad generalizations. So far as the large groups are concerned, there appears to be no correlation between taxonomic position and structural complexity on the one hand, and the number, length, width, or volume of the chromosomes on the other. But it is generally agreed that within restricted circles of affinity the number of chromosomes, as well as their size and form, may often afford important evidence in the determination of genetic relationships.[1]

This latter conclusion is strongly suggested by the fact that such euploid and aneuploid numbers as are seen to characterize mutants arising in cultures of diploid plants are found also in the several varieties or species of certain genera and families. Attention has above been called to the remarkable euploid series in *Chrysanthemum*, *Rosa*, *Triticum*, and other genera; here the related species in each genus exhibit various multiples of some fundamental haploid number of chromosomes. In other groups aneuploid series are found. A conspicuous example is the genus *Carex*, in which the species examined show 22 chromosome numbers, all but one of which lie between 9 and 42 (Heilborn, 1922, 1924) (Fig. 179). Taxonomic relationship is here clearly reflected in the number and size of the chromosomes.

It is a striking fact that polyploidy is much less prevalent among animals than among plants. Although triploid and other polyploid individuals are frequently encountered, animal cytologists have found comparatively few cases in which related species or varieties differ regularly in the number of their basic chromosome sets. This situation is not fully understood; but one of the chief reasons for the rarity of polyploidy in animals appears to lie in the fact that in them the sexes are usually separate, owing to the operation of a mechanism whereby sex factors are segregated in meiosis and combined in syngamy, whereas plants are very commonly monœcious, sex in such organisms not being so closely dependent on chromosome distribution (Muller, 1925). In harmony with this interpretation, to which more explicit reference will be made in the discussion of sex-chromosomes (p. 451), is the fact that polyploidy in plants appears to be more often associated with monœcism than with diœcism, the latter now being known in several instances to involve sex-chromosomes.

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[1] See McClung (1908), Strasburger (1910*b*), Farmer and Digby (1914), Tischler (1916, 1921–1922), Winge (1917), Gates (1920*b*, 1924*ab*), Marchal (1920), Meek (1920), and Heilborn (1924). A general review of the cytology of plant hybrids is given by Tischler (1925).

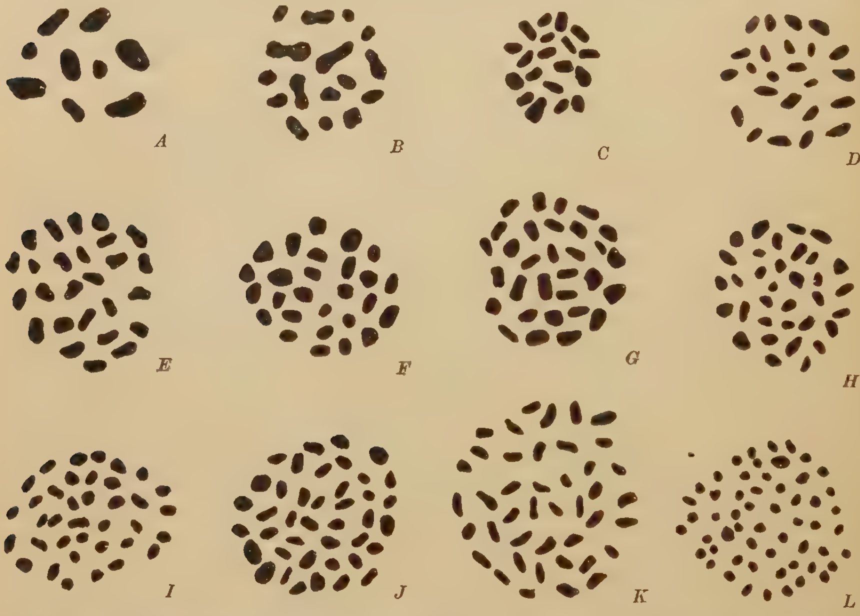

FIG. 179.—The chromosomes in the metaphase of the first meiotic mitosis in the microsporocytes of various species of *Carex*, illustrating aneuploidy. *A*, *pilulifera*, 9 chromosomes. *B*, *sparsiflora*, 16. *C*, *montana*, 19. *D*, *tomentosa*, 24. *E*, *digitata*, 26. *F*, *loliacea*, 27. *G*, *caryophyllea*, 29. *H*, *punctata*, 34. *I*, *distans*, 37. *J*, *vesicaria*, 41. *K*, *Goodenoughii*, 42. *L*, *hirta*, 56. (*After Heilborn*, 1924.)

Of special interest are certain current investigations on the morphology of the chromosome sets of related species and genera. In *Crepis*, which has come to be a favorite genus for cytological and genetical studies,[1]

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[1] Juel (1905); Rosenberg (1909, 1918, 1920); Digby (1914); Babcock and Collins (1920); Babcock, Clausen, Collins, and Mann (1922); Collins and Mann (1923); M. Nawaschin (1915, 1925); W. R. Taylor (1925*c*), Mann (1925).

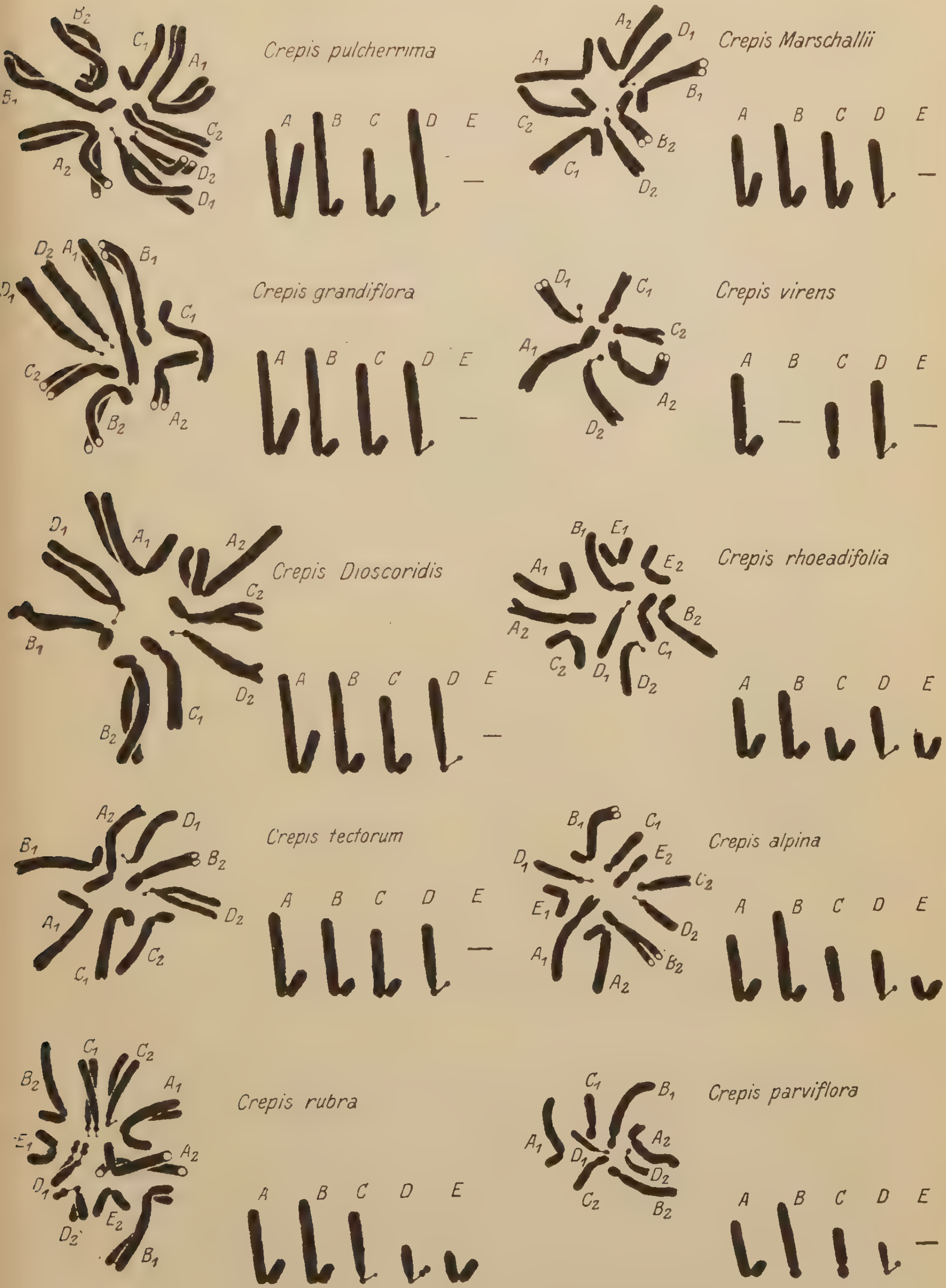

FIG. 180.—The chromosomes in 10 species of *Crepis*. Diploid complement in root cell at left; haploid set at right. (*After M. Nawaschin*, 1925*a*.)

most of the species have only three, four, or five pairs of chromosomes. As the result of an examination of ten of these species M. Nawaschin (1925) has concluded that the chromosomes are of five distinguishable kinds as regards size and shape, and that each of the species has a characteristic diploid complement made up of from three to five of these chromosomes in pairs (Figs. 180, 181). Of the five kinds of chromosomes, four (*ABCE*) have two arms, and differ in the absolute and relative length of these arms, while the fifth (*D*) has a terminal knob to which is attached a satellite on a pedicel. *A*, *C*, and *D* occur in all of the ten species investigated; *B* is present in all but *virens* (*capillaris*); *E* is found in only three species. It is further observed that a given chromosome may vary considerably in length in the complements of the different species. The fact that the order of the species, when arranged in a series on the basis of a progressive lengthening or shortening of a given chromosome of the set, may differ from the order in a series similarly arranged for a different chromosome is taken to mean that the chromosome set is not a simple unit, but is rather a harmonious system of autonomous entities which are in some measure independent of one another in their evolutionary alteration. Studies now being carried on in this genus by several investigators promise to throw an interesting light on the problem

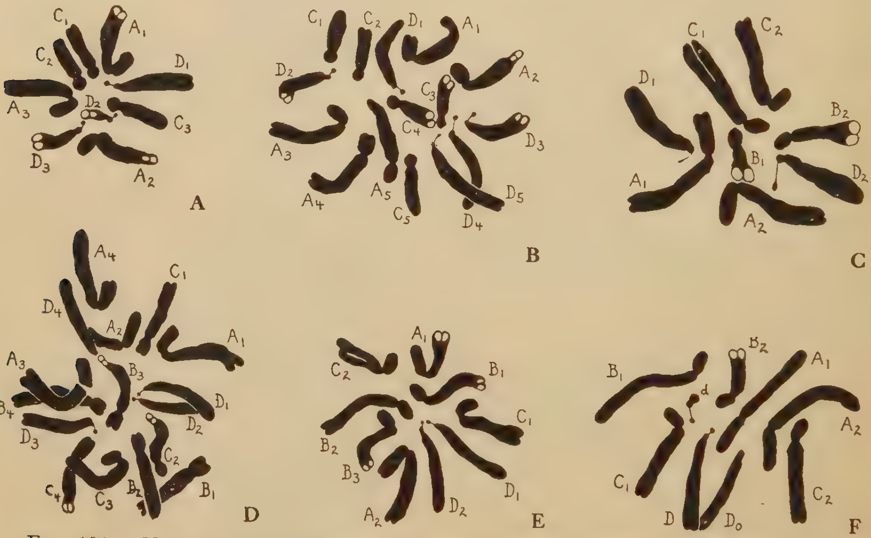

FIG. 181.—Chromosome phenonema in somatic cells of *Crepis*. *A*, triploid group in *Crepis capillaris*, showing three *A*-, *C*-, and *D*-chromosomes. *B*, pentaploid group in *C. capillaris*, showing five chromosomes of each type. *C*, diploid group in an "asymmetrical" individual of *C. Dioscoridis*, showing *D*-chromosomes with unequal satellites. *D*, tetraploid group in *C. tectorum*, showing four *A*-, *B*-, *C*-, and *D*-chromosomes. *E*, diploid group in an individual of *C. tectorum* having an extra *B*-chromosome. *F*, diploid group in an individual of *C. tectorum* with the *D*-chromosome segmented into two portions: $D_o$ and *d*. (*After M. Nawaschin*, 1925*b*.)

of the specific rôles of individual chromosomes in development and heredity.

Special mention should also be made of the siutation in the three related genera *Gasteria*, *Aloë*, and *Haworthia*. The chromosome complement in all three genera consists of four long and three short pairs, but in each genus there are minor peculiarities (Fig. 64) (W. R. Taylor, 1925*b*).

Very often a genus with a euploid series of species includes also one or two species having one or two pairs more or less than one of the euploid numbers. Sometimes a genus includes two or more euploid series with different basic numbers. Examination of the other characteristics of these chromosomes only serves to emphasize the fact that related species or varieties are characterized by "related" chromosome complements, and that chromosome characters within families or genera have an unquestionable taxonomic significance.

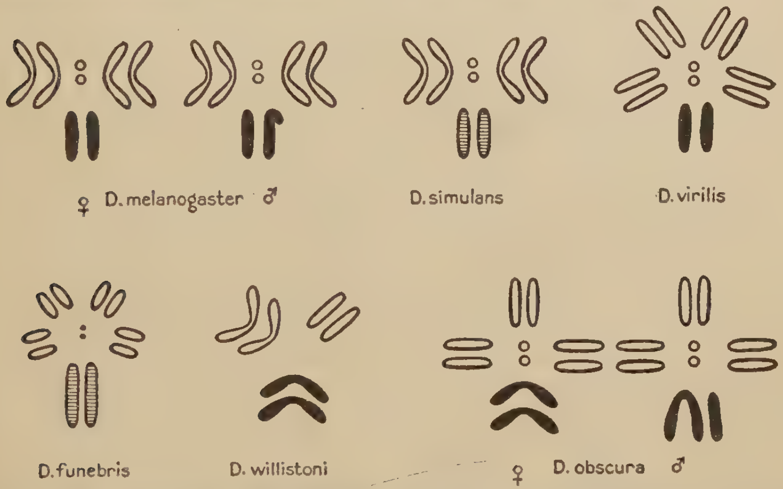

Fig. 182.—The somatic chromosome complements of several species of *Drosophila*. Pairs known to be sex-chromosomes shown in solid black; those presumed to be are marked with cross lines. (*After Metz, Moses and Mason*, 1923.)

Similar evidence is afforded by animals. In the Drosophilinæ, including 27 species of *Drosophila*, there are 13 known types of chromosome groups, all of which bear a general resemblance to one another, but show characteristic minor differences (Fig. 182) (Metz, 1914; Metz and Moses, 1923). It appears probable that the 13 types have been derived from one or two original types by segmentation of chromosomes and other aberrations. A remarkable instance of similarity in the chromosome complements throughout a large group is afforded by the Acrididæ, a family of grasshoppers studied by McClung, Robertson, and others. In about 100 genera, including 800 species, the diploid number in nearly all cases is 24 in the female and 23 in the male (the female has two sex-chromosomes and the male one). Moreover, the chromosomes of the complement uniformly show a comparable order of sizes (McClung, 1924). It is stated that the degree of relationship is as clearly expressed in the chromosomes as in the externally visible characters, and that the evidence indicates a descent by variation from a common ancestral series of chromosomes paralleled by corresponding variation in somatic structures (Robertson, 1916).

The numerical and size relationship shown by chromosomes of related species is of itself a suggestive fact. When to this is added the fact that alterations in the chromosome complement have repeatedly been shown to coincide with changes in the organism's other characters (*Œnothera*, *Datura*, *Primula*, *Drosophila*), and the further fact that such changes may be experimentally induced, it at once becomes clear that the determination of the manner and causes of such alterations is one of the most momentous problems in biology, for these changes afford one clue to the means by which diversity in the organic world has been brought about. Hence the recent renewal of interest in chromosome complements on the part of the taxonomist, who describes and classifies what has evolved, and the geneticist, who attempts to ascertain more directly how it has evolved. How, then, do the alterations in question take place?

**Tetraploidy.**—The mode of origin of the tetraploid from the diploid condition is one of the most important to be ascertained, since tetraploidy, like triploidy, may often be a preliminary to the production of other euploid and aneuploid numbers. Several observations and suggestions have been made as follows.

*Chromosome Splitting without Nuclear Division.*—The doubling of the diploid number by a splitting and non-separation of the chromosomes has been called "non-division" (Bridges, 1924). Such a process has been thought to occur most frequently in the zygote, a tetraploid individual resulting immediately. This explanation was suggested by Rosenberg (1907, 1909, 1917) for *Hieracium*, *Taraxacum*, and *Rosa*, and has been regarded as a probable one by many writers.[1] The evidence that the doubling occurs in the zygote is indirect, but nevertheless strong. It has been induced in animal eggs by shaking or by treatment with KCl during cleavage. In somatic cells non-division has been clearly observed: in the roots of *Spinacia oleracea* de Litardière (1923*c*) finds not only cells with 12 chromosomes, the normal diploid number, but also cells with 24 and 48. Usually the chromosome halves remain closely associated through the prophase and separate normally in the anaphase; but in other cells they become independent of each other and undergo a second splitting, so that 24 chromosomes pass to each daughter nucleus. The process may be repeated, giving octoploid nuclei. The cause of this aberration is unknown. The same observer also finds "didiploid" nuclei in *Cannabis* (1924). Lesley (1925) reports the occasional presence of both diploid and tetraploid cells in the root tips of certain tomato plants.

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[1] Gates (1909*b*, 1913, 1924*a*) and Davis (1911) for *Œnothera* and other genera; Strasburger (1910) for *Œnothera* and *Wikstrœmia;* Tischler (1910) for *Musa;* Sax (1921, 1922) for *Triticum;* Tahara (1921) for *Chrysanthemum;* Afzelius (1924) for *Senecio;* Winge (1917).

In *Zea Mays* Randolph (1926) has observed occasional tetraploid microsporocytes undergoing meiosis in the anther along with normal diploid ones. The origin of the tetraploid condition is not known here, but non-division is suggested. Likewise, in the testis of an insect, *Euschistus variolarius*, Bowen (1922*f*) saw tetraploid cells which had arisen through some mitotic aberration, possibly non-division; and in these cells meiosis occurred. In neither *Zea* nor *Euschistus* has the subsequent history of the "reduced" but diploid nuclei been fully traced, but in *Zea* the occasional appearance of triploid plants strongly suggests that functional diploid gametes may thus arise and lead to polyploidy. The origin of tetraploidy through a fusion of two such gametes would, of course, depend on the occurrence of the aberration in the lineage of both sperms and eggs. It will be readily recognized that in a monœcious plant a single aberration of this type occurring before the differentiation of the carpellate and staminate portions might result in the production of diploid gametes of both sexes; whereas in a diœcious plant, or in a monœcious one following the differentiation of the carpels and stamens, two instances would be required for the production of tetraploidy in the immediate offspring. Chromosome doubling in sporogenous cells probably more often leads to triploidy.

*Transverse Segmentation of Chromosomes.*—In a tetraploid type of *Primula Kewensis* Farmer and Digby (1914) observed that the chromosomes were only half as large as those of the diploid type, and they held with Strasburger (1910) that such a condition must be due to the transverse segmentation of all the chromosomes. Heilborn (1924), however, attributes it to a limit in the cell's capacity for producing chromatin: if the chromosomes become more numerous from any cause, each of them must be smaller, as seems to be the case in *Carex*. Many observers admit the probability of transverse segmentation in certain cases of aneuploidy, but it does not now seem probable that tetraploidy arises in this way.

*Nuclear Fusion.*—A doubling of the chromosome number through nuclear fusion may be conceived to occur in several ways. Strasburger (1910) and Ernst (1918) thought it not unlikely that the daughter nuclei of the first mitosis in the zygote might reunite. Such a fusion of daughter nuclei in sporocytes has been reported several times. Thus in *Œnothera* (Gates) and *Hieracium* (Rosenberg) the nuclei may apparently fuse during the telophase of the second meiotic mitosis. In the second sporocyte division in *Rosa* Blackburn and Harrison (1921) observed one giant spindle instead of two normal ones, indicating that the mitotic figures may unite. This seems clearly to take place in *Papaver* (Ljungdahl, 1922). The result would be diploid spore nuclei, but the condition in the subsequently formed gamete nuclei is unknown. Non-division might easily be mistaken for nuclear fusion; in fact, the two processes probably merge into each other. Tetraploidy in graft hybrids of *Solanum* is thought by Winkler (1916) to be due to the fusion of nuclei in cells near the wound, the migration of nuclei into adjacent cells having been induced in other plants by mechanical injury (Miehe, 1901; Schweidler, 1910). The rôle of such a process in nature is questionable (Ernst, 1918).

*The Union of Diploid Gametes following Ameiosis.*—Not only may diploid gametes arise from diploid individuals after meiosis in abnormally tetraploid cells as above described, but they are also known to be formed as a result of the complete failure of meiosis. This is regularly the case in many apomictic organisms (p. 355), such a process commonly preceding the parthenogenetic development of diploid eggs. That the union of two such diploid gametes, occasionally produced by an organism usually showing meiosis and sexual reproduction, may account for certain cases of tetraploidy seems not unlikely. This was adopted by Stomps (1912) and Ernst (1918) as the probable interpretation for *Œnothera*, as opposed to that of Gates. In the case of *Datura*, however, it does not conform to the genetic evidence (Blakeslee).

*The Hybridization Theory.*—Since the origin of the tetraploid condition through chromosomal aberrations in diploid organisms is a change which leads to other irregularities and the production of further modifications of the chromosome complement, it is particularly desirable to account for those initial aberrations. Reference was made in Chapter XVI to the fact that apomictic phenomena are often attributed to hybridization, and that ameiosis and polyploidy are common accompaniments of such asexual modes of reproduction. Although there are probably several causes of aberrations resulting in doubling the chromosome number, it is the view of Ernst (1917, 1918), Winge (1917), and a number of other investigators[1] that polyploidy, like apomixis, has one of its chief causes in hybridization. Ernst and Winge, two of the principal exponents of this theory, point out that it is highly improbable that a simple reduplication of a specifically pure complement of chromosomes through splitting would result in the qualitative changes seen in many tetraploid forms. Quantitative differences might be expected, as in polyploid moss plants produced by regeneration (Marchal), but scarcely any qualitative alterations of evolutionary importance. They hold rather that those aberrations in diploids which result in tetraploidy, partiularly non-division and ameiosis, are due to the hybrid constitution of the chromosome complement in which they occur: the chromosomes of this complement are of two specifically different origins, and are therefore to some degree incapable of that harmonious action in pairs which is assumed by Winge to be necessary for proper development and reproduction (*cf.* p. 357).

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[1] Rosenberg (1917), I. Holmgren (1919), Täckholm (1920, 1922), Jeffrey *et al* (1922), Afzelius (1924), Gates (1924).

The process of chromosome doubling is conceived by Winge as follows. When two specifically different haploid chromsome sets of like number are brought together in a gametic fusion, they may act in complete harmony at all stages, and the result is a new sexually reproducing form (*e.g., Ribes;* Tischler, 1906). If the harmony is somewhat less, the chromosomes, after having coöperated in pairs throughout development, may separate after a temporary synaptic association in the sporocytes and then split longitudinally, thus giving rise to diploid spores and gametes (many known cases). Finally, if the harmony is insufficient for the "pair action" necessary to development, all of the chromosomes in the zygote may split longitudinally, the resulting halves then acting in pairs throughout the development of the resulting tetraploid sporophyte. If this sporophyte produces diploid gametes after meiosis, the result may be a sexually reproducing tetraploid form; if meiosis fails, the gametes will be tetraploid also, and the result in this case may be an apomictic tetraploid form. Both of these conditions are observed in nature, and the interpretation harmonizes well with phenomena in apomictic diploids (p. 356).

This process, which Winge calls "indirect chromosome binding," involves a splitting of all the chromosomes, and may thus be regarded as a form of reduplication; but it differs from the simple reduplication of Strasburger and others in that it is due to the hybrid constitution of the complement that so becomes doubled, which accounts for the qualitatively new characters observed here but not expected after the simple reduplication of a pure complement. In certain tetraploid forms the size relations of the chromosomes seem to indicate the origin of the condition through hybridization rather than simple reduplication; but in others the tetraploid complements are clearly composed of four complete haploid sets, which suggests the reduplication of all of the chromosomes originally present in the diploid form. The cause of such doubling may in some cases lie in the hybridity of the diploid complement, but in other instances it seems probable that other agencies must be responsible for the change.

Whatever may be the underlying cause of the change from diploidy to tetraploidy, and from this to octoploidy, the rôle of hybridization in the production of intermediate multiples and of aneuploidy is unmistakable.

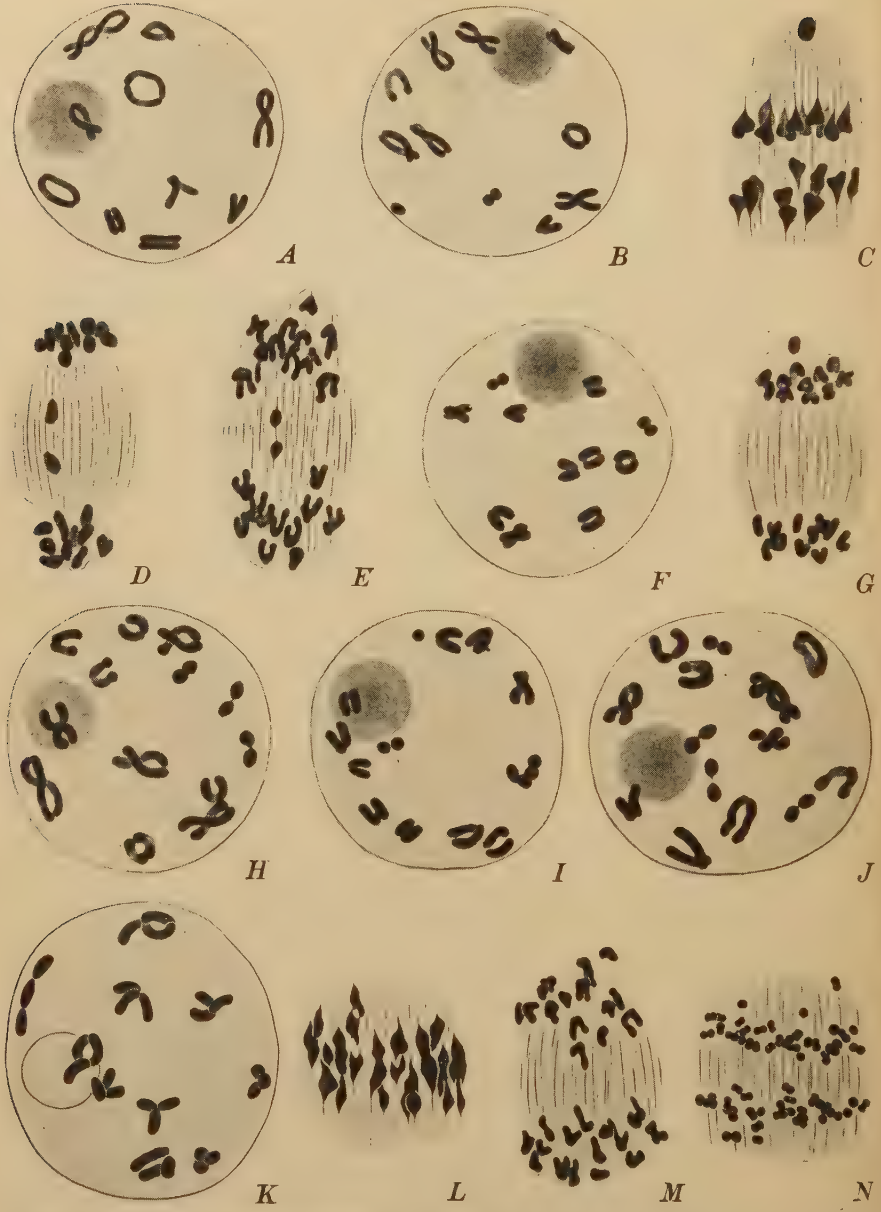

FIG. 183.—Chromosome phenomena in the microsporocytes of *Zea Mays*. In certain cultures, plants with more than the usual number of chromosomes occur more or less frequently. In the same plant, variations in number are observed very rarely. *A*, diakinesis, showing 10 bivalent chromosomes, the usual number. *B*, 10 bivalents and one unpaired univalent. *C*, unpaired chromosome passing to one pole in mitosis *I*. *D*, unpaired chromosome separating equationally in *II*. *E*, unpaired chromosome separating equationally in *I*. *F*, 11 bivalent chromosomes. *G*, anaphase of *I* in plant with 11 bivalents and one unpaired chromosome. *H*, 13 bivalents. *I*, 13 bivalents and one unpaired chromosome. *J*, 14 bivalents. *K*, diakinesis in triploid plant, showing 10 trivalents. *L*, metaphase *I* in same. *M*, anaphase *I* in same; the 30 elements tend to be distributed equally, as shown. *N*, single large mitotic figure occasionally observed in microsporocytes of triploid plant; 30 elements, presumably chromatids, in each group. (*From Randolph*, 1926. *Figure kindly loaned in advance of publication elsewhere.*)

**Triploidy.**—Triploidy has in nearly all cases been attributed to the union of a haploid with a diploid gamete. Triploids have been produced at will in several genera by crossing diploids with tetraploid mutants, varieties, or species;[1] and there is abundant genetical and cytological evidence to show that this also occurs naturally. Frequently the diploid gamete arises from the same type or even the same individual that produces the haploid one.[2] In either case the resulting individual has three sets of chromosomes. Such crossings are without doubt directly or indirectly responsible for most cases of triploidy.

In *Hyacinthus* de Mol (1923) observed that diploid plants occasionally produced a few functional diploid pollen grains, apparently as a response to physiological conditions induced by an artificial shortening of the growing season. When other diploid varieties were pollinated with such pollen a few triploid seedlings appeared among the many diploid ones. De Mol thinks it probable that abnormal physiological states may play a larger rôle than has been supposed in causing chromosome doubling in other genera. The mechanism of the process is not known in *Hyacinthus*.

Another possible cause of triploidy is dispermy, or the entrance of two male nuclei into the egg. Such a process has been observed in *Gagea* (Némec, 1912) and *Œnothera* (Ishikawa, 1918), though its actual results are unknown in these cases. Tischler (1916), Ernst (1918), and Winkler (1920) regard dispermy as a probable second cause of triploidy. Triploid larvæ have been experimentally produced through dispermy in certain animals (p. 179).

**Other Polyploids.**—The higher polyploids, such as pentaploids, hexaploids, octoploids, and so on, may be accounted for on the basis of chromosome doubling like that giving origin to tetraploidy, together with crossings of the several forms so arising. A hexaploid, for example, might arise by a doubling of the chromosomes in a triploid hybrid through non-division in the zygote; or by the union of triploid gametes following ameiosis in a triploid (haplosis sometimes fails thus in *Datura*); or by dispermy followed by a doubling in the triploid zygote (Ernst, 1918).

In *Rosa*, Blackburn and Harrison (1924*b*) found that when *R. pimpinellifolia* (14 chromosomes in ♀ gamete) was crossed with *R. tomentosa* (7 in ♂ gamete) the resulting fertile plant was *R. Wilsoni* with 42 chromosomes rather than the expected 21. In this case, therefore, hexaploidy arose as the result of doubling in a hybrid between a tetraploid and an unbalanced pentaploid (*tomentosa* produces sperms with 7 chromosomes and eggs with 28). In *Papaver*, Ljungdahl (1924) produced a stable hexaploid type by crossing a diploid (7 in gamete) with a decaploid (35 in gamete). In *Triticum*, Kihara (1919) produced pentaploids by crossing tetraploids (Emmer) with hexaploids (Spelt). The cytological features of these hybrids, which will soon be discussed further, parallel so precisely those of polyploid forms found in nature that there can be no doubt that hybridization, together with a doubling often attributable in turn to hybridity, has acted as an important cause in bringing about the numerical chromosome relationships observed in related species.

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[1] *Œnothera semigigas* (*Lamarckiana* × *gigas*) (Geerts, 1911; Stomps, 1912; Gates, 1913); *Drosera* (Rosenberg, 1909); *Datura* (Blakeslee *et al.*); *Triticum* (Sax, 1922*a*).

[2] *Hieracium* (Rosenberg, 1917); *Eupatorium* (I. Holmgren, 1919); *Morus* (Osawa, 1920); *Hyacinthus* (de Mol, 1923); probably *Zea* (Randolph, 1926).

**Haploidy.**—The mode of origin of the haploid mutants of *Datura* has not been determined cytologically. That they are the result of haploid parthenogenesis seems highly probable in view of the fact that when such mutants appear after an interspecific cross they are always purely maternal in character. It is of interest to note that the appearance of haploid mutants is more frequent when the plants are subjected to low temperatures.

The meiotic chromosome behavior in these haploid *Datura* mutants is of considerable interest. The 12 chromosomes undergo no synaptic pairing and are distributed irregularly in the first mitosis. Usually the distribution is more or less equal, the spore cells after *II* having numbers not far from six. Occasionally, however, spores are formed with all 12, and these give rise to functional gametes. By selfing such plants one can obtain diploid individuals which are completely homozygous, except for possible gene mutations.

These haploid plants afford an instance of the origin of one type from another with a higher chromosome number. Similarly, Blakeslee has observed the production of diploids in crosses between tetraploids and diploids; and Håkansson (1924*a*) reports the origin of a diploid from a tetraploid in *Œnothera*. In neither of these cases is the mechanism of the process known. It is none the less evident that the series may sometimes progress from higher numbers to lower, as well as from lower to higher as in the majority of known cases.

**Aneuploidy.**—Some of the aberrations responsible for numerical changes not involving entire sets of chromosomes, will now be described. A discussion of the manner in which they lead to the production of stable aneuploid forms will be given in the next section.

*Non-disjunction.*—One of the most commonly observed phenomena concerned in the production of aneuploidy is non-disjunction, originally discovered by Bridges (1913). In this process two chromosomes which would normally pass into two daughter nuclei fail to separate in the anaphase, and pass together to one pole of the achromatic figure. Such aberrations may occur in either the somatic or the meiotic divisions. Considering only one pair of chromosomes, the immediate results are as follows: in a meiotic division one daughter nucleus contains both members of the pair, while the other contains neither; in a somatic division in diploid tissue one nucleus contains three chromosomes instead of a pair, while the other contains but one.

The most frequent cause of the appearance of individuals with one chromosome more or less than the normal diploid number is non-disjunction in one of the meiotic divisions, commonly the first of these. Gametes (or spores followed by gametes) with an extra chromosome, or lacking a chromosome, are occasionally formed along with the normal ones; and a union of a haploid gamete with an $n + 1$ gamete, for example, will give a $2n + 1$ individual. The best-known cases of this are the *Œnothera* mutants of the *lata* group (15 chromosomes), the 12 primary $2n + 1$ *Datura* mutants (25 chromosomes), and the occasional non-disjunctional forms of *Drosophila*, with 7 or 9 chromosomes rather than 8 (p. 468). In *Datura* Belling and Blakeslee saw eight cases of non-disjunction in 1,137 microsporocytes. Belling (1925) observed ten cases in three buds of *Uvularia*. Other examples of this process are seen in *Crepis* (Rosenberg, 1918, 1920; Babcock, 1924), *Matthiola* (Frost and Mann, 1924), and *Senecio* (Afzelius, 1924); and further instances might be cited. It is obvious that types with unpaired chromosomes will usually show certain irregularities in meiosis, so that non-disjunction must ordinarily be followed by other adjustments before stable aneuploid types can be established. Frequently two $n + 1$ gametes having the same member of the complement in duplicate may meet, the extra chromosomes then behaving as an additional homologous pair in the offspring. That such aberrations may involve the same pair repeatedly is suggested by certain individuals of *Zea Mays*, in which Randolph (1926) observes a sexavalent group in addition to the normal 10 pairs.

*Reduplication of Chromosomes.*—The increase in chromosome number by a longitudinal division of some of the members of the complement is held to be probable in certain cases. Sax (1921) adduces evidence in favor of this interpretation for *Triticum*. Heilborn (1922, 1924) attributes the remarkable aneuploid series in *Carex* to the splitting of some of the chromosomes following their failure to undergo normal synapsis.

*Segmentation of Chromosomes.*—The transverse division of chromosomes, usually at constriction points, has been repeatedly reported, particularly in cells subjected to abnormal conditions (p. 180). That such a segmentation is responsible for the origin of certain classes of aneuploid forms appears not unlikely in view of the researches of Metz (1914, 1916, 1918) on the Drosophilinæ, Hance (1918) on *Œnothera*, Marchal (1920) on *Campanula*, Seiler and Haniel (1921) and Seiler (1922) on *Lymantria* and *Solenobia*, and Gotoh (1924) on *Secale*. Comparisons of the chromosome complements leave little doubt on this point in some cases. For example, in *Secale* there are normally seven pairs of chromosomes, and measurements of the chromosomes in occasional plants with eight pairs seem clearly to indicate a segmentation of two of the largest members at median constriction points. The segmentation hypothesis is supported by genetic evidence also in the Drosophilinæ (Metz, Moses, and Mason, 1923). Heilborn (1924) assigns a rôle to the segmentation of long chromosomes in the formation of the fundamental chromosome set of *Carex*. In a culture of *Zea Mays* Randolph has frequently observed one or two "diminutive" chromosome pairs, which are quite distinct from the ordinary 10 pairs and any unpaired elements. They are transmitted regularly to the next generation, where more of them may appear than were present in the two parents together. Their origin has not been determined with certainty; but it has been observed that in the first meiotic anaphase small undisjoined portions of bivalents may linger at the equatorial plane and remain connected with the larger disjoined portions by attenuated strands of chromosome substance. Such undisjoined portions bear an extremely close resemblance to the diminutives. It accordingly seems highly probable that the origin of the diminutive chromosomes is to be attributed to the segmentation of certain members of the regular complement.[1]

*Fusion or Loss of Chromosomes.*—The temporary union of chromosomes to form complexes resembling single units is frequently reported (p. 181). That such unions may become permanent and so result in types with decreased chromosome numbers has been held by certain workers. Thus de Litardière (1922) derives the 19-chromosome species of *Senecio* from 20-chromosome species. This interpretation is questioned by others (*e.g.*, Afzelius, 1924), who regard non-disjunction or the loss of chromosomes in irregular mitoses as a more plausible explanation. Metz (1916) is uncertain as to which phenomenon may be responsible for the absence of the smallest chromosome pair in some species of *Drosophila*. It was the opinion of Marchal (1920) that the three-chromosome condition in certain species of *Crepis* should be attributed to a fusion of chromosomes in a four-chromosome species, but the studies of M. Nawaschin (1925) on the morphology of the chromosomes in this genus appear to preclude this explanation. *Crepis virens*, with three pairs of chromosomes, plainly lacks a pair present in the other species examined by this investigator (Fig. 180). On the basis of chromosome morphology he further opposes the view that the five-chromosome condition has arisen either by duplication through splitting or non-disjunction, since the extra chromosome is unlike any in the four-chromosome species. It is in hybridization that Nawaschin sees the probable cause of the numerical relationships in the chromosome complements of *Crepis*.

*Hybridization.*—The crossing of forms with chromosome sets which do not act harmoniously when brought together is unquestionably one of the chief causes underlying the production of aneuploid as well as euploid species and varieties. Not only is it primarily responsible for the occasional evidences of disharmony, such as weak synaptic attraction, in forms otherwise regular in their cytological and genetic behavior, but it leads to a considerable series of irregularities frequently terminating in the production of stable types with chromosome numbers unlike those of the original parents.

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[1] Unpublished observations.

**Chromosome Behavior in Hybrids.**—During the past few years the literature in this department of cytology has grown enormously. A complete review of it here is obviously out of the question, so that we shall simply cite certain typical cases illustrating the chief significant modes of chromosome behavior. This, together with the descriptions of phenomena in hybrids already given incidentally, will serve as an introduction to this important subject.

*Types with Unequal Parental Numbers.*—The irregularities in chromosome behavior in hybrids and in other forms with deranged chromosome mechanisms are particularly evident at the time of synapsis. Most striking and characteristic are the aberrations seen in hybrids between forms with different chromosome numbers, as has already been pointed out in the chapter on meiosis (see p. 280). It will be convenient here to distinguish five modes of synaptic behavior, though it should not be thought that these are sharply distinct.

1. Because it is so highly characteristic of hybrids, the "*Drosera* type" of meiosis may be mentioned first. The chromosomes of one parental derivation conjugate with an equal number of those of the other parental derivation, thus forming as many bivalents as there were univalents in the smaller gametic complement; the remaining univalents of the larger gametic complement are left without synaptic mates. Many instances of this type of synapsis are known, but the behavior of the bivalents and unpaired univalents in the ensuing mitoses is not the same in all.[1] In some cases (*Drosera*) they may be irregularly distributed as wholes to the two poles in the first mitosis, but usually they split and separate. In the *Caninæ* section of the genus *Rosa* the seven bivalents in the microsporocyte disjoin and pass to the poles as usual, after which the split univalents (14, 21, or 28 in number) move to the equatorial plane and then separate (Fig. 184). Some of the daughter univalents may lag behind and fail to be included in the daughter nuclei. In the second mitosis all of the chromosomes, including those which were previously paired and those which were not, may split,[2] but ordinarily some of the

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[1] A tabulation of the various kinds of behavior shown by unpaired univalents in the first meiotic mitosis is given by Täckholm (1922, p. 261).

[2] This is one of the few known cases which show that a chromosome may undergo two splittings during a single meiosis. It has also been observed in certain *Hieracium* hybrids (Rosenberg, 1917).

latter again fail to reach the daughter nuclei. Moreover, the lagging chromosomes may form small nuclei about which small supernumerary microspores are organized. In the megasporocyte all of the univalents pass to one pole in *I* and divide in *II*, so that two of the megaspores have many chromosomes (28 in a pentaploid hybrid), while the other two have only 7. The embryo sac is formed here by a 28-chromosome spore. These roses are not sexually fertile, but reproduce by nucellar embryony.

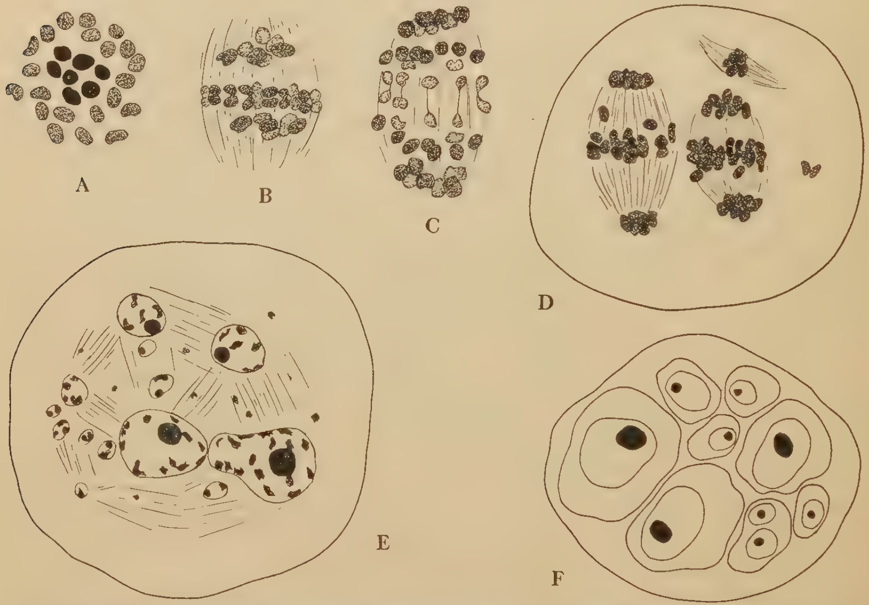

FIG. 184.—Chromosome behavior in *Rosa* hybrids. *A*, polar view of the chromosomes in the metaphase of the first meiotic mitosis in the microsporocyte of *R. glauca dilatans*, showing 7 bivalents surrounded by 21 univalents. *B*, anaphase of mitosis *I* in *R. glauca plebeia;* the bivalents have disjoined and the split univalents lie at the equator. *C*, late anaphase in *R. pomifera Grenieri*. *D*, division *II* in *R. Junzillii;* chromosomes which failed to reach poles in *I* have formed an extra mitotic figure. *E*, telophase of *II* in the same, showing the formation of supernumerary nuclei. *F*, polyspory (more than 4 spores) resulting from mitotic irregularities in *R. pomifera*. (*After Täckholm*, 1922.)

In pentaploid *Triticum* hybrids (Emmer 14 + Vulgare 21 = 35) the 14 bivalents first disjoin, the 7 univalents then splitting and passing to the poles, as in *Rosa* (Fig. 185, *D*) (Sax, 1922*a*; Watkins 1924). In *II* the 14 previously paired chromosomes split, but the 7 others are distributed irregularly without dividing. In triploid hybrids (Einkorn 7 + Emmer 14 = 21), according to Sax, the 7 univalents pass undivided to the poles in advance of the 7 bivalents, and in *II* all are split. Sax finds that sterility in these hybrids increases with the number of unpaired univalents present in meiosis, many non-functional spores being produced. In the next generation the sterility is even greater, because of the somatic weakness attributable to the deranged nuclear mechanism.

Since gametes and segregates with abnormal numbers tend to be eliminated through sterility, the ultimate fertile segregates have either 14 or 21 chromosomes (Sax, 1921, 1923). Those with 14 largely resemble the Emmer parent, while those with 21 are more nearly like Vulgare. This seems to indicate that factors in the 7 additional chromosomes are chiefly responsible for the Vulgare characters (Sax and Gaines, 1924). Extensive studies on *Triticum* have also been made by Kihara (1919, 1921, 1924, 1925), who reports a somewhat less regular synaptic behavior in some of his material. In triploid hybrids, for example, he finds that the number of bivalents varies from 4 to 7, and that of the univalents accordingly from 13 to 7. In the megasporocytes of wheat hybrids Watkins (1925) reports the occurrence of aberrations similar to those in the microsporocytes. In *Avena* hybrids with 35 chromosomes (*barbata* 14 + *fatua* 21) Dorsey (1924) has observed that the 7 univalents split and pass to the poles in advance of the disjoining 14 bivalents in *I*, and segregate at random after the 14 divide in *II*.

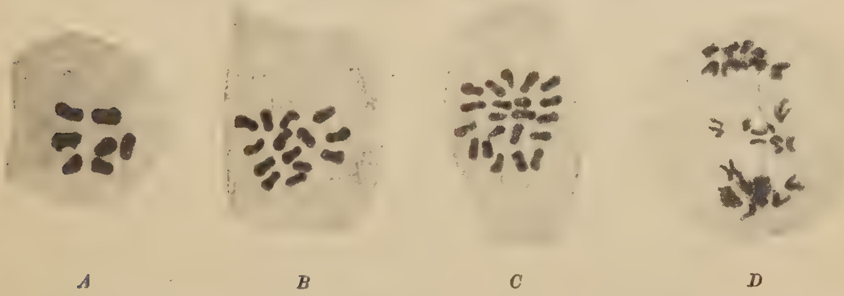

FIG. 185.—The chromosomes of *Triticum*. *A*, metaphase of division *I* in *T. monococcum;* 7 chromosomes. *B*, *T. durum;* 14 chromosomes. *C*, *T. vulgare;* 21 chromosomes. *D*, division *I* in hybrid between members of Emmer group ($n = 14$) and Vulgare group ($n = 21$); the 14 bivalents have disjoined and the 7 univalents are separating equationally. (*After Sax*, 1922*a*.)

2. In certain hybrids the chromosome numbers are such that one cannot be sure that the pairing members are derived from the two parental complements. It is to be borne in mind that synapsis depends on homology rather than parental derivation, so that one may expect the chromosomes contributed by one parent occasionally to undergo synapsis *inter se* if such a contribution comprises more than a single fundamental haploid set. This "autosynapsis," or "autosyndesis," actually occurs at times, as, for example, in certain *Crepis* hybrids (Collins and Mann, 1923). In a type with 24 chromosomes (4 *setosa* + 20 *biennis*) 10 bivalents and 4 univalents appear in the microsporocytes, which is taken to mean that the *biennis* chromosomes have undergone synapsis *inter se*, leaving the 4 of *setosa* unpaired. The resulting spores and gametes carry 10 *biennis* chromosomes and from 0 to 4 *setosa* chromosomes, as judged by the numbers appearing in the next generation.

In *Crepis*, therefore, both bivalents and univalents are formed, as in mode 1, but here the chromosomes of the smaller gametic complement are not involved in synapsis.

3. A third mode of synapsis in hybrids is exemplified in *Papaver* (Ljungdahl, 1924), *Digitalis* (Haase-Bessell, 1921), and *Solanum* (Winkler, 1916). It appears that all of the chromosomes undergo synapsis, irrespective of the number contributed by either parent—both autosynapsis and allosynapsis occur (p. 281). For example, in *Papaver* hybrids with 42 chromosomes (7 *nudicaule* + 35 *striatocarpum* or *radicatum*) there are 21 gemini at diakinesis. A transition to this from mode 1 is seen in *Viola* (J. Clausen, 1922). In *Viola* hybrids with 30 chromosomes (13 *tricolor* + 17 *arvensis*) there may be 13, 14, or 15 bivalents. Such cases show that if homologues are present among the chromosomes not pairing with those of the other parental complement, they may pair with each other; and if they behave regularly thereafter, a new stable type with a larger number of chromosomes may be established.

4. Frequently the synaptic pairing is for some reason deficient, very few or no gemini being formed; in fact, a series may be arranged between mode 1, with definite numbers of bivalents and univalents, and meiosis with no synapsis whatsoever. In some cases, typifying what may be called mode 4, the chromosomes are distributed more or less irregularly in *I* and usually split in *II*. Such a behavior is seen in *Hieracium lævigatum* (Rosenberg, 1917) and *Erigeron* cfr. *annuus* ♂ (I. Holmgren, 1919). In hybrids arising from crosses between *Zea Mays* (10 pairs) and *Euchlæna perennis* (20 pairs) Longley (1924*c*) reports that trivalents, bivalents, and univalents appear at meiosis, the 30 chromosomes being irregularly distributed in the two mitoses. The inconstant pairing of extra chromosomes has also been observed in *Zea* by Randolph (1926).

5. Finally, after no synaptic pairing the chromosomes may all undergo a longitudinal splitting in the ensuing mitosis, which is therefore equational rather than disjunctional. This has been observed in *Hieracium pseudoillyricum* (Rosenberg) and *Erigeron* cfr. *annuus* ♀ (Holmgren).

*Types with Equal Parental Numbers.*—Not only in hybrids between forms with unlike chromosome numbers, but also in those with equal parental numbers, and in many types not suspected of being hybrids, various irregularities may occur. It has already been pointed out that chromosome sets of unlike derivation may coöperate more or less harmoniously in a hybrid. Thus when crosses are made between *Zea Mays* and *Euchlæna mexicana*, each of which has 10 pairs of chromosomes, the hybrid shows 10 regular bivalents in the microsporocytes (Longley, 1924*c*). It has also been shown how, according to a theory proposed by Winge, lack of harmony may lead to polyploidy (p. 397). One of the commonest chromosomal aberrations observed in relatively stable hybrids, as well as in apparently non-hybrid forms, is non-disjunction.

As a result of this process, spores and gametes with one or two chromosomes more or less than the usual number arise, and such gametes may unite either with normal gametes or with others of their kind. A conspicuous example is *Datura*, in which a considerable series of $2n + 1$ types is known (p. 388). These arise through the union of normal with $n + 1$ gametes following non-disjunction. If two such $n + 1$ gametes unite, the resulting 26-chromosome plant has 10 chromosomes present in duplicate and 2 in triplicate; or, if the 2 extra chromosomes happen to be homologous, 11 in duplicate and 1 in quadruplicate. When four homologous elements are present they may segregate at random in meiosis (*Datura*) or behave as two distinct pairs (*Triticum*). In this manner new types with one or more chromosome pairs above the usual number may arise. Similarly, types with one or two pairs less than the normal number might arise through the union of two $n - 1$ gametes following non-disjunction, but for some reason types lacking chromosomes are rarer than those with extra ones.

Aberrations other than non-disjunction, such as the irregular distribution of chromosomes after deficient synaptic pairing, also occur in types with equal parental numbers. For example, in *Raphanus* × *Brassica* hybrids there is no synapsis, though each parent contributes nine chromosomes (Karpechenko, 1924). The incompatibility of chromosomes is due to something more fundamental than mere number. Comparative studies on many organisms have led directly to the conclusion that both deficient synapsis and non-disjunction, followed by the synapsis of homologous extra chromosomes and the elimination of any that are without homologues, have been very potent factors in the production of groups of species or varieties with differing chromosome numbers.

In hybrids of both classes—those with like and those with unlike parental chromosome numbers—the irregularities at meiosis lead to the production of many weak and functionless spores and gametes. The ability to function depends in various degrees upon the character of the chromosome complement in different cases. Frequently the functional gametes may show a wide range of variation in their complements, while in other instances only those with certain chromosome assortments will come to maturity and act in syngamy. Wide departures from the normal complement usually result in abortion. An interesting situation is found in triploid *Œnotheræ*, according to van Overeem (1921, 1922[1]). Here the functional eggs apparently have chromosome numbers ranging all the way from 7 to 14, but the male gametes have only 7 or 14, owing to the abortion of pollen grains with the intermediate numbers. In *Zea Mays* it is evident that microspores and male gametes with various numbers of extra chromosomes are functional, for the offspring of crosses between types showing such aberrations exhibit a surprising range in the number of extra paired and unpaired elements (Randolph, 1926).

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[1] This paper has an extensive bibliography of works on *Œnothera*. See also the review by Oehlkers (1924).

The union of gametes with such a variety of chromosome complements naturally leads to great diversity in the following generations. Many combinations do not result in viable forms, but others give rise to types which develop normally until meiosis, when chromosomal aberrations may again appear. In successive hybrid generations meiotic irregularity and genetic instability are observed as long as extra unpaired chromosomes are present. These tend to be eliminated gradually through irregular mitoses, until relatively stable types with one or more numbers of regular chromosome pairs are established. Frequently in the course of such adjustment through elimination of extra chromosomes some members of the complement become lost while others are duplicated, so that, although the chromosome number of one of the original parents may be restored, the assortment is a new one and the plants are correspondingly altered in character. This again emphasizes the fact that it is the qualitative constitution of the complement, rather than the mere number of chromosomes, that is of primary significance in species alteration. The hybridization of forms with more or less incompatible chromosome complements has unquestionably played a prominent rôle in the differentiation of many taxonomic groups. This is becoming increasingly apparent as chromosome aberrations, defective and supernumerary pollen grains, sexual sterility, polyploidy, and other characteristics of known hybrids are found more and more frequently in nature.[1]

**Apomixis.**—The possibility of apomixis is always to be borne in mind in interpreting genetic and taxonomic data. This has been made especially evident by the outstanding work of Täckholm (1920, 1922) on *Rosa*. In the *Caninæ* section of this genus there are types which have long been regarded as distinct species because of their remarkable constancy in external characters and the lack of intermediate types. Täckholm has found that the section includes tetraploid, pentaploid, and hexaploid forms, and that they all show most strikingly the *Drosera* type of chromosome behavior in meiosis. As a result the microspores and male gametes in the pentaploid forms, for example, contain from 7 to 22 chromosomes, while the eggs usually have 28. This clearly indicates the hybrid nature of these *Caninæ* roses. Why, then, are they so stable genetically? It turns out that they are apomictic: the embryo arises not from the sexual cells but by budding from the nucellus. The *Caninæ* types are therefore not species, but asexually reproducing clones, which maintain their hybrid chromosome complements and the same external characters from generation to generation because the reassorting of chromosomes and genes at meiosis plays no part in the production of the next generation.

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[1] *Cratægus* and *Rubus* (Longley, 1923, 1924*ab*); American species of *Rosa* (Penland, 1923); *Salix* (Blackburn and Harrison, 1924*a*); *Callitriche* (C. Jörgensen, 1923).

Täckholm adduces evidence to show that the original acts of hybridization occurred long ago, and that the genetic diversities which have since appeared in the apomictic lines are to be attributed chiefly to somatic mutations. Apomixis obviously retards the process of forming new combinations, but it preserves new types once they are formed, just as in the case of other vegetatively propagated plants. The importance of such facts for students of the origin of species and varieties can scarcely be overestimated.

**Conclusions.**—The observational and experimental evidence reviewed in this chapter indicates that distinct heritable changes in the characters of organisms may involve Mendelian recombinations of genetic factors or genes, actual mutations of these genes, alterations in the number and assortment of chromosomes as results of aberrations in mitotic behavior, and hybridization, by which many new combinations are produced. Any stable sexual type is characterized by a chromosome complement consisting of a certain number and assortment of elements showing individual functional and morphological differences; all of them constitute a harmonious system. Any change in the constitution of this system, whether quantitative or qualitative, large or small, is accompanied by a corresponding alteration of the type.

With regard to the rôle of genes and their mutation in the origin of species, Morgan (1923*c*) points out that the inheritance of gene mutations as Mendelian characters suggests that Mendelian differences in general have originated through such mutations. "It is . . . now clear that these smaller mutant variations must be those small heritable variations that Darwin himself appealed to as furnishing the materials for organic evolution." These must not be confused with non-inherited environmental variations. In reply to the objection that changes due to gene mutations are too trivial to be of significance in evolution, Morgan further points out that the minor characters used by the geneticist and the taxonomist may often be superficial secondary results of changes which have some invisible but more fundamental physiological effects with an actual survival value. The systematist of necessity differentiates many species on the basis of characters which have played no part in the actual production of those species.

Change of type is effected not only by such mutations of genes and their Mendelian recombination through normal chromosome distribution, but also by more extensive and less orderly alterations in the grouping and interaction of inheritance materials through abnormalities in chromosome behavior. Non-division, non-disjunction, segmentation, and other aberrations all play rôles in the production of new chromosome complements, which differ from the original complement in the number, size, and assortment of their constituent elements. The range of such variation is greatly increased by crossing among the altered types. It seems abundantly evident that hybridization involving types with chromosomes that are in some measure incompatible is one of the chief causes of chromosomal aberrations leading to the establishment of qualitatively new gene systems. The irregularities in chromosome behavior immediately following such crossing gradually disappear in subsequent inbred generations through the elimination of unpaired chromosomes, until there remains a chromosome complement whose members act in harmony, although they together may constitute a very new type of interacting system.

In more general terms, hybridization, or outcrossing, plays its chief rôle by inducing variability in immediately subsequent generations, the amount of variability depending on the degree of constitutional difference between the types involved. If free intercrossing with the parental and other types continues, the variability is kept up. There is also evidence that genes are more mutable when in the heterozygous condition. In order for stable types to differentiate from the series of variants, crossing must be restricted by some form of isolation—natural or artificial selection, geographic isolation, intersterility, and the like, whereupon some of the inbreeding types rapidly become stable. The origin of species is thus frequently conceived as a fixation of stable independent types through the inbreeding of variable types originally resulting from hybridization.

Since hybridization has long been recognized as an important cause of diversity in organisms, it may be well to summarize the contributions which cytology has made in this connection. Cytology has shown the close relation between hybridization and polyploidy, between polyploidy and a certain class of mutations, and hence between hybridization and such mutations. In its elucidation of chromosome aberrations in hybrids it has thrown much light on the curious behavior of inherited characters in hybrid lines: the apparently non-Mendelian inheritance in crosses between species, varieties, and mutants; the unexpected gametic ratios frequently obtained; the unlikeness of reciprocal hybrids; sterility; and a variety of otherwise unintelligible phenomena. It has heightened the precision with which certain changes in character can be attributed to crossing, often affording a direct clue in the case of suspected hybrids. It has shown the value of cytological data in determining taxonomic relationships within narrow circles of affinity, and the prime necessity of utilizing such data in many problematic cases. It has shown the importance of apomixis and somatic mutation as factors in heredity, and hence their importance to the geneticist and field taxonomist. In short, cytology has afforded a common rationale for a great variety of phenomena hitherto studied by distinct groups of biologists.

## CHAPTER XVIII

## EMBRYONIC CHARACTERS AND CYTOPLASMIC INHERITANCE

In the present chapter will be considered two subjects which have an interesting bearing on the problem of the rôle of the protoplasmic organs in heredity. First: the literature of experimental biology contains numerous accounts of researches designed to test the nuclear theory. The results of some of these experiments, which were carried out largely on animal eggs, seemed to indicate the inheritance of certain embryonic characters through the cytoplasm primarily; but it will be seen that these results are now subject to another interpretation. Second: a comparatively clear instance of inheritance otherwise than through the nucleus appears to have been found in a class of chlorophyll characters in plants.

Animal eggs which are inseminated in water outside of the body constitute peculiarly favorable material for the study of the mechanism of heredity, for such eggs usually have a large volume of cytoplasm, while the male gametes which unite with them are almost wholly nuclear in composition. The eggs of echinoderms, amphibians, and fishes have been very extensively used in such experiments. Those of echinoderms are especially favorable because of the ease with which they may be kept under experimental control *in vitro*, and the readiness with which they unite with spermatozoa of foreign species or genera. Moreover, the insemination of enucleated egg fragments may be accomplished with no great difficulty. Eggs or egg fragments with paternal chromosomes only may be obtained by shaking the eggs before insemination (sea urchins: Boveri), by cutting the egg into pieces after the entrance of several spermatozoa (chiefly amphibians: Spemann, Baltzer, G. and P. Hertwig), or by killing the egg nucleus with radium (amphibians: G. and P. Hertwig). The results of such experiments have varied with the species used, the methods, and the direction of the crosses; but, in general, they have tended to support the nuclear theory. Some of the hybrid larvæ show the characters of both parents. More instructive are those which are matroclinous or patroclinous, especially when viewed in the light of their cytological features.[1]

**Matroclinous Hybrid Larvæ.**—The fact that so many echinoderm hybrids are largely or wholly similar to the female parent in their larval characters would at first sight seem to discredit or seriously weaken the nuclear theory of heredity. But it has been found that the failure of paternal characters to appear is coupled with a partial or complete failure to function on the part of the nuclear matter introduced by the spermatozoön. Some of the observed modes of behavior are as follows.

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[1] For accounts of experiments of this general nature, see Morgan (1924*a-g*), Conklin (1924), G. Hertwig (1920*ab*), P. Hertwig (1923), Stomps (1923), and Wilson (1925). The material in this portion of the chapter has been selected largely from these works.

1. The parental nuclei do not fuse; the ♂ material degenerates in the egg cytoplasm: *Echinus* ♀ × *Mytilus* (mollusk) ♂ (Kupelwieser, 1912). This has the appearance of induced parthenogenesis.

2. The ♂ material is extruded from the nucleus after the fusion of the parental nuclei: *Echinus* ♀ × *Chætopterus* ♂ (Godlewski, 1911).

3. Most of the ♂ material is extruded during the first and second cleavage mitoses: *Strongylocentrotus* ♀ × *Sphærechinus* ♂ (Baltzer, 1910); *Echinus* ♀ × *Adouinia* ♂ (annelid) (Kupelwieser, 1912).

4. The ♂ material is eliminated later: in the first several cleavage divisions, as in *Hippnoë* ♀ × *Toxopneustes* ♂ (Tennent, 1912); or in the blastula stage, as in *Echinus* ♀ × *Arbacia* ♂ (Baltzer).

The elimination of the paternal chromosomes as cleavage proceeds is largely the result of their tendency to lag behind the maternal chromosomes, so that they fail to be included in the daughter nuclei. This is a common thing in hybrids. In her work on fish hybrids Pinney (1918, 1922) relates this lagging to the viscosity of the egg cytoplasm, which is unfavorable to the sperm chromosomes; hence the first block to normal development appears to be a physical factor. In many cases it is obvious that the foreign spermatozoön can stimulate development without being able to function in further growth and differentiation.

In all of the above examples the larvæ continue to develop for a time presumably with the haploid number of chromosomes (maternal), after the elimination of the paternal chromosomes has been accomplished. The following class of cases is interesting in this connection.

5. No elimination of the paternal chromosomes may occur; the larvæ are diploid, yet maternal in character: *Sphærechinus* ♀ × *Arbacia* ♂; *Strongylocentrotus* ♀ or *Echinus* ♀ × *Antedon* ♂ (Baltzer, 1910). This was attributed by Baltzer to a latency of the ♂ nuclear matter: the paternal chromosomes can coöperate with the maternal chromosomes in mitosis, but they fail to exert any hereditary effect upon larval characters. Ernst (1918) has suggested that such cases may possibly represent the induced development of diploid eggs.

6. Finally, in some hybrids there is complete compatibility between the two parental groups of chromosomes, and the larvæ are intermediate in character: *Sphærechinus* ♀ × *Echinus* or *Strongylocentrotus* ♂ (Baltzer, 1910; compare with the reciprocal cross in class 3).

Taking all of the foregoing six classes together, it is seen that the maternal character of the larvæ is correlated with the fact that only the maternal nuclear elements are functioning normally; when the paternal chromosomes coöperate fully the larvæ show paternal characters as well. Such cases therefore confirm rather than discredit the nuclear theory. It should be said that this discussion does not include those characters which are so far along with their differentiation in the egg before syngamy that no spermatozoön would be expected to affect them. Such characters will be considered later.

The hereditary rôle of the chromosomes is strikingly shown in certain experiments performed by Herbst and by Tennent. By treating eggs of *Sphærechinus* with valerianic acid Herbst (1909) caused them to undergo cleavage. While the cleavage mitosis was in progress a spermatozoön of *Strongylocentrotus* was allowed to enter the egg, where it at once gave rise to its group of chromosomes (Fig. 186). These, however, arriving too late to join regularly in the mitosis, were incorporated in neither of the daughter nuclei of the first cleavage. They resumed the form of a nucleus, and this was included in one of the blastomeres. This blastomere therefore contained two nuclei, one maternal and one paternal, which combined during the subsequent stages; whereas the other blastomere had a maternal nucleus only. Herbst regarded such nuclear behavior as responsible for the frequently found larvæ which were hybrid in character on one side and purely maternal on the other. This experiment has been held to show not only that it is the nucleus of the spermatozoön which brings in the paternal factors, but also that it is the chromosomes alone that are responsible. It is assumed that the other nuclear material, such as karyolymph, which may be present, as well as any cytoplasmic elements, have opportunity to mix generally with the egg cytoplasm, since the membrane of the male nucleus breaks down and leaves the chromosomes lying free before the egg divides into the two blastomeres. The paternal characters, however, appear only where the paternal chromosomes come to be located, that is, in one-half of the organism.

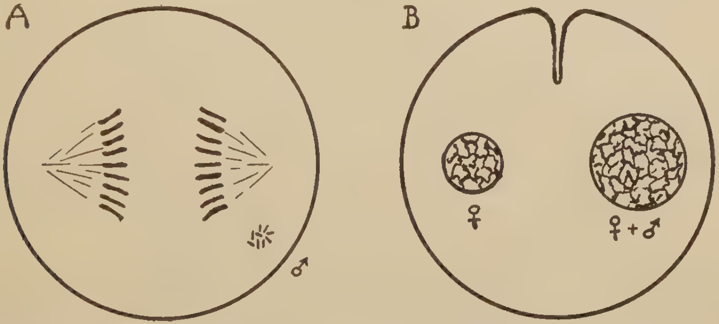

Fig. 186.—*A*, egg of *Sphærechinus* undergoing artificially induced cleavage mitosis; spermatozoön of *Strongylocentrotus* has entered and formed its chromosomes. *B*, cytokinesis beginning; one blastomere will have a purely maternal nucleus, and the other will have a hybrid nucleus. (*Based on work of Herbst*, 1909.)

Tennent (1910, 1912) found an interesting situation in certain reciprocal crosses. In *Hippnoë* ♀ × *Toxopneustes* ♂ the paternal chromosomes are eliminated and the larvæ are matroclinous, whereas in *Toxopneustes* ♀ × *Hippnoë* ♂ there is no elimination and the larvæ are patroclinous. Here the *Hippnoë* nucleus determines the character of the larvæ in both crosses: the cytoplasm is from *Toxopneustes* in one case and from *Hippnoë* in the other, but in both the differentiation is of the *Hippnoë* type. Tennent observed further that in the second cross the larvæ showed more maternal characters when the acidity of the medium was increased. Landauer (1922) reports an effect of ammonia on the parental characters of echinoderm larvæ. This again emphasizes the conception of the organism and the environment as constituting a single system. In the nuclear theory of heredity it is not assumed that the cytoplasm and the environment have no influence upon the development of the heritable characters, but only that the nucleus under ordinary circumstances has an especially pronounced differential effect upon this development.

"Maternal hybrids" occur also in plants, the new individuals developing after pollination being wholly like the female parent. It has been demonstrated cytologically in the case of *Atamosco* (Pace, 1913), and experimentally in the tetraploid forms of *Primula Kewensis* (Pellew and Durham, 1916), that such plants are *false hybrids:* pollination merely causes the parthenogenetic development of an egg already diploid through a failure of meiosis, and the male elements are in no way incorporated. It was seen in the preceding chapter that in plants, as well as in animals, the maternal and paternal chromosomes may show various degrees of incompatibility in hybrids.

**Merogony.**—It has been very difficult to obtain cogent evidence for or against the nuclear theory by inseminating enucleated egg fragments with foreign sperm. Boveri at one time thought he had patroclinous echinoderm larvæ with only paternal nuclear material, but later concluded that truly enucleate inseminated fragments in this cross (*Sphærechinus* ♀ × *Echinus* ♂) are unable to reach the pluteus stage (larva). In *Sphærechinus* ♀ × *Strongylocentrotus* ♂ he succeeded in getting plutei from inseminated egg fragments, but the plutei of the two genera were so much alike that the hybrids afforded little evidence on the question of the rôle of the nucleus; they only showed that the cytoplasm of one genus with the nucleus of another genus can form a pluteus. Godlewski (1906) obtained a matroclinous pluteus, using egg fragments of *Parechinus* and sperm of *Antedon*. This appeared to demonstrate the hereditary rôle of the cytoplasm, but Boveri (1918) later showed that the egg fragments in this case were in all probability not devoid of maternal nuclear material as Godlewski had supposed. Tennent (1912) observed that in some cases the maternal rather than the paternal chromosomes were eliminated, the larvæ showing a corresponding patroclinous tendency. Patrocliny in *Œnothera* was at one time attributed to merogony, but Renner (1913, 1914) showed this to be an error.

The weakness of haploid embryos, upon which comment was made in the preceding chapter, is one of the principal reasons for the failure of merogonic larvæ to answer decisively the question of the relative rôles of the nucleus and the cytoplasm in determining the characters which appear early in the ontogeny. Moreover, interpretation is rendered still more difficult by the fact that the differentiation of many such characters is under way in the egg before syngamy. Such embryonic characters in the immediate hybrid would accordingly be expected to be maternal in type to a degree depending upon the extent to which this differentiation had been carried out before the entrance of the spermatozoön. This leads to a consideration of cases in which embryonic characters are thus foreshadowed in the *promorphology* of the egg (see Conklin, 1924; Morgan, 1924*afg*; Wilson, 1925).

**The Promorphology of the Egg.**—In many eggs there are indications of a definite polarity in the location of the nucleus and in the stratification of visible oöplasmic substances before syngamy, or even before meiosis. Furthermore, a bilateral symmetry is also sometimes evident in the peculiar shape of the egg (some insects), or in the position of colored oöplasmic substances. There is much reason to believe that in many eggs not showing such visible indications, polarity and symmetry are nevertheless present, and are not later induced by the path of the sperm nucleus, which, however, usually does influence the plane of the first cleavage. As differentiation continues, usually just after syngamy and before cleavage, the egg substances become arranged in "patterns" which are characteristic of the various phyla (Fig. 187) and which appear to bear a rather close relation to the normal differentiation of embryonic parts.

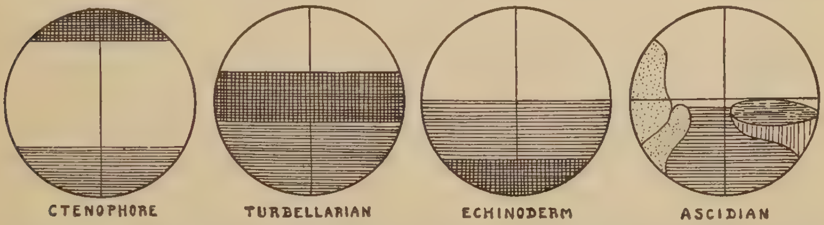

Fig. 187.—Eggs of various animals, showing the patterns assumed by the oöplasmic materials. In the first three the initial cleavage has occurred, and the plasmas becoming ectoderm, mesoderm, and endoderm are represented in clear white, cross-hatching, and parallel ruling respectively. In the fourth egg two cleavages have occurred, and several definitely arranged substances are present. (*After Conklin*, 1915.)

If such eggs are placed in a centrifuge the visible oöplasmic substances may be thrown into unusual positions, and the effects of such changes upon development are most instructive. In *Styela*, an ascidian, Conklin

(1915, 1917) found that such displacements always result in abnormal development, many curious monstrosities being obtained. The variously colored oöplasmic materials have often been called "organ-forming substances." In other animals (echinoderms, annelids, gastropods) the results are quite different: here the nucleus, centrosome, yolk, and all other oöplasmic substances can be displaced without modifying normal polarity, symmetry, and development. This indicates that the fundamental organization of the egg resides not primarily in the visible oöplasmic materials, but in a comparatively immovable cytoplasmic structure—in a cortical ectoplasmic layer and an internal framework of spongioplasm, according to Conklin (1924). Here the colored oöplasmic materials are not so closely bound up with the fundamental organization as they are in *Styela*, and are clearly not themselves "organ-forming substances." In either case it seems that "at the time of fertilization the hereditary potencies of the two germ cells are not equal, all the early stages of development, including the polarity, symmetry, type of cleavage, and the pattern, or relative positions and proportions of future organs, being foreshadowed in the cytoplasm of the egg cell, while only the differentiations of later development are influenced by the sperm" (Conklin, 1915).

The question at once arises as to how far this cytoplasmic organization may be due in turn to nuclear activity during the formation of the egg. May not the larval characters already developing before fertilization be ultimately as dependent on nuclear factors as are any other characters? The promorphology of the egg is developed through reactions involving both the cytoplasm and the diploid biparental nuclei of the mother.[1] Although the characters directly dependent on this promorphology may not be affected by the paternal nucleus in the immediate hybrid, one should expect such an effect on these characters in subsequent generations, in the development of which the new paternal material has a share. Thus an embryonic character inherited "maternally" in any particular first generation hybrid because of the late addition of the male nucleus, should show biparental inheritance through subsequent generations.

The evidence so far obtained on this point is in accord with these expectations. For example, in cross-fertilized sea urchin or fish eggs the rate and the type of cleavage are the same as in the mother, no matter what the direction of the cross; they are characters impressed upon the egg during its ovarian history, and the male nucleus fails to change the condition already induced in the egg by its own nucleus. When the hybrid matures and produces eggs, however, it is found that these all show the dominant rate and type of cleavage. This shows that the male does affect the character in the second generation. (It also shows that the influence of the dominant factors present in the egg during its development lingers after they are extruded into the polar bodies in maturation, since all the eggs show the dominant type of cleavage in spite of the fact that half of them must have lost the factors in meiosis in the hybrid. This after-effect is of short duration, however.) Breeding experiments with moths and butterflies (Toyama, 1913; Tanaka, 1916; Uda, 1923) have shown similar results with respect to embryonic characters (see Morgan *et al.*, 1922, and Morgan, 1924*ag*).

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[1] It is here that significance may attach to the interchanges involving basophilic substance, or "chromidia" (p. 237).

The general conclusion is that embryonic characters whose differentiation is initiated in the egg cytoplasm before syngamy are as dependent on the nucleus as are other characters. They are fundamentally Mendelian in behavior, but they are peculiar in that *the visible effect of the male gamete is delayed for a generation.* "There is every expectation that, given sufficient time, the nucleus will determine the character of the structures produced by the cytoplasm" (Morgan, 1924*f*). It therefore turns out that the question of the effect of the nucleus on embryonic characters which merogonic larvæ failed to answer decisively has been definitely settled by Mendelian crosses involving single differences.

**Cytoplasmic Inheritance.**—The only known instances of inheritance seeming at present to be clearly independent of nuclear factors are found among the many cases of transmitted "chlorophyll characters" in plants. It is obvious that two successive generations of cells reproducing by division resemble each other because the organs of any given cell may actually become the corresponding organs of the daughter cells. Thus in the case of a unicellular green alga the daughter individuals are like the mother individuals in being green because the chloroplast of the mother cell is divided and passed on directly to them. In those algae in which a swarm spore germinates to produce a multicellular individual (*Ulothrix*, etc.), or associates with others of its kind to form a colony (*Hydrodictyon, Pediastrum;* Harper, 1908, 1918*ab*), the color of the successive colonies or multicellular individuals is a "metidentical" character transmitted directly by the repeated division of chloroplasts. Hence, as Harper urges, the nucleus is not required here to account for the resemblance between successive generations of cells or individuals, so far as this character is concerned.

A similar interpretation has been placed by many geneticists upon the inheritance of chlorophyll characters in the higher plants, the supposition being that plastids, multiplying only by division, are responsible for the distribution, in the individual plant and through successive generations, of those characters which manifest themselves in these organs. Abnormalities in chlorophyll coloring, such as pale greenness, whiteness, and variegation, are accordingly held to be due to an abnormal condition or behavior of the chloroplasts. Researches on plants showing such abnormalities have brought to light the interesting fact that the chlorophyll characters fall into two distinct categories, although they may appear outwardly very much alike: those of one category are inherited strictly according to Mendelian rules, while those of the other are not. Often both types occur in the same genus,[1] or even in the same species.

It is only with the non-Mendelian category that the present discussion is concerned. We shall list a few representative cases according to a classification drawn up by Demerec,[2] and then mention certain theories which have been proposed to account for the various modes of behavior observed.

1. *The inheritance is maternal.*

   *a.* The variegated plants when selfed or crossed produce variegated, green, pale-green, and white offspring.

The most widely known example of this class is *Mirabilis jalapa albomaculata*, described by Correns (1909*a*). In plants of this race there are some branches with normal green leaves, some with white leaves, and some with variegated leaves. Flowers are borne on branches of all three types. In all cases crosses between unlikes result in seedlings with the color of the maternal parent. For instance, if a flower on a green branch is pollinated with pollen from a flower on a white branch, the offspring are all green. In the reciprocal cross the offspring are all white, and soon die because of the lack of chlorophyll. If flowers on variegated branches are pollinated, offspring of all types result. In no case does the pollen affect the color of the progeny.

A similar condition has been found in *Stellaria media* (the most fully analyzed of all cases), *Senecio*, *Taraxacum*, *Hieracium*, *Arabis*, and *Mesembryanthemum* by Correns (1919, 1922); also in *Antirrhinum* (Baur, 1907, 1910), *Melandrium* (G. H. Shull, 1913), *Primula* (Gregory, 1915), *Zea Mays* (E. G. Anderson, 1923), and certain other genera.

*b.* The variegated plants produce only variegated progeny irrespective of the type of pollen used: *Humulus japonicus albomaculata* (Winge, 1919).

*c.* The affected plants produce only self-colored (green or pale green) progeny: *Glycine hispida* (Terao, 1918).

2. *The inheritance is biparental.*

*a.* Crossings between flowers on the green and the white parts of the variegated plant may result in green, white, and variegated offspring; selfing variegateds results only in white offspring. The type case in this class is *Pelargonium zonale albomarginata* (Baur, 1909, 1919). This form, which is characterized by white-margined leaves, often has pure-green and pure-white branches, as does *Mirabilis*. Crosses either way between flowers on these two kinds of branches may result in variegated offspring; inheritance is here not purely maternal as in *Mirabilis*. A case of variegation observed by Stomps (1920) in *Œnothera biennis* probably belongs in this class.

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[1] *Zea Mays* (Emerson, Lindstrom, Demerec, Gernert, Miles, Collins and Kempton, *et al.*); *Capsella*, *Ipomœa*, *Urtica*, and *Mercurialis* (Correns); *Melandrium*, *Aquilegia*, and *Antirrhinum* (Baur); and certain other genera. For the situation in *Zea Mays*, see Lindstrom (1923) and Demerec (1923).

[2] Unpublished. See also the somewhat similar classification by Winge (1919*a*).

*b*. Crossing and selfing plants exhibiting the abnormality result only in variegated offspring: *Capsicum annuum* (Ikeno, 1917).

There may thus be distinguished four principal classes of non-Medelian chlorophyll inheritance, since the two kinds of segregation: (*a*) of both self and variegated individuals and (*b*) of variegateds only, are combined in both ways with two modes of inheritance: (1) maternal and (2) biparental. Explanations which have been offered to account for such phenomena are consequently somewhat divergent.

With regard to the "albomaculata type" of variegation (1*a*), it is the hypothesis of Correns that the condition is due to a cytoplasmic disease which affects or destroys the chloroplasts. It is therefore delivered directly to the next generation through the egg cytoplasm, and is not transmitted by the male parent because the male gamete introduces no cytoplasm into the egg. If it were due to nuclear factors it would be transmitted equally by both parents, since the nuclear contributions of the two are equivalent. The variegated patterns are due to the unequal distribution of healthy and diseased cytoplasm during the cell-divisions involved in development. The case is analogous to bacterial diseases transmitted directly through animal eggs, and is not to be confused with ordinary heredity.

Baur (1919) admits the view of Correns for the albomaculata type (1*a*), but for the "albomarginata type" (2*a*) he holds to his early view (1909) that the appearance of green and white tissues is due to the presence of two distinct kinds of plastids or their primordia, green and white, which are sorted out as the cells multiply by division. These plastids Baur assumes must be contributed by both parents. This, in general, is the interpretation adopted by Gregory for *Primula* (1*a*) and by Ikeno for *Capsicum* (2*b*); it is also favored by E. G. Anderson (1923) for maternal strains of maize (1*a*).

Winge (1919) has advanced the hypothesis that in forms segregating greens, whites, and variegateds the defect is in the plastids themselves, whereas in those giving rise to variegateds only it is in the cytoplasm in which the plastids lie; and, further, that the two modes of inheritance, biparental and maternal, are due to the fact that in some cases the male gamete introduces cytoplasm into the egg, while in others it does not. It is on this basis that he classifies the known cases of non-Mendelian hereditary variegation.

An explanation of a very different type has been suggested by certain geneticists who believe these peculiar forms of chlorophyll inheritance to be fundamentally Mendelian and therefore associated with nuclear factors. Their unusual hereditary behavior is attributed to a segregation of allelomorphic factors in somatic divisions, *i.e.*, by such a segregation as is ordinarily supposed to occur only at sporogenesis. This hypothesis has been employed by Bateson (1919), E. J. Collins (1922), and in a special way by Stomps (1920) for variegation, and also by certain zoölogists for phenomena occasionally observed in animals (*e.g.*, Newman, 1917, on the armadillo).

The cytological evidence bearing on the foregoing theories is as yet rather meager. Green and colorless plastids have frequently been observed in variegated plants, but too little is known about their origin and behavior to warrant generalizations. Randolph (1922) has made a critical study of the situation in *Zea Mays*. In normal plants and in several Mendelian and non-Mendelian abnormal chlorophyll types he found the same kind of visible structure in the meristematic cells: all contain very minute protoplastids (plastid primordia) which, so far as the microscope shows, are of one kind. In normal plants the protoplastids develop into large green chloroplasts, whereas in pale-green, yellowish, or white plants, or in the various regions of variegated plants, they fail to attain the normal color, the normal size, or both. No evidence was found that green and colorless plastids represent fundamentally distinct types. On the contrary, they appear to be end results of different modes of development of one type of initial body; moreover, they are connected by a series of all conceivable intermediate conditions, particularly in cells on the boundary between green and white areas in variegated leaves. Hence no support is found for the hypothesis that plastids of two types undergo a sorting out during the development of the tissues. Why it is that the primordia develop so differently in different cells can only be conjectured, but it appears probable that their peculiar behavior is an indication of some invisible differentiation being carried out in the cytoplasm. It is natural to think of chondriosomes in this connection, but there is at present no evidence that they are concerned. The obscurity surrounding the origin of proplastids (p. 110) adds a further element of uncertainty to any theory involving plastid behavior.

Noack (1922) made a study of the development of the leaf of *Pelargonium*, and concluded that the cell lineage is such as would rule out Baur's explanation of the albomarginata type of variegation on the basis of a sorting out of two sorts of plastids. In view of Noack's later work (1924), however, his results are open to another interpretation, according to Demerec.

At the present time there is comparatively little cytological foundation for the view that variegation involves a somatic segregation of Mendelian factors. Development regularly involves the differentiation of unlike tissues, but that this is accompanied by a segregation of unlike allelomorphic factors does not now seem probable. The occasional non-separation of split chromosomes has been observed in somatic tissues. Such aberrations undoubtedly result in certain occasional instances of somatic mutation, but it is questionable whether they ever occur with sufficient regularity to aid in accounting for the definite and widespread phenomena described above. In this connection the case of *Adiantum cuneatum* (I. Anderson, 1923) is of interest. In the gametophyte as well as the sporophyte there are both green and pale areas, characterized respectively by the presence of green and pale plastids in the cells. In the gametophyte the differentiation of the two sorts of tissue could hardly involve the segregation of allelomorphic factors, since the tissue is haploid unless the species is a polyploid one.

That the biparental and maternal types of non-Mendelian plastid inheritance may be correlated respectively with the entrance and non-entrance of paternal cytoplasm into the egg does not seem improbable in view of the available descriptions of syngamy in angiosperms (p. 331). But nothing can be stated with assurance until much more has been learned concerning the history of cytoplasm and cytoplasmic inclusions throughout the life cycle.

**Conclusion.**—On the basis of all the available evidence one is justified in concluding that the nucleus is the cell organ chiefly responsible for the phenomena of heredity. That the organic inheritance is thus largely in the form of chromosomal factors causing character differences to be inherited in the Mendelian manner now seems to be well established. One of the main present problems is that of determining how widely Mendelian principles apply to the many characteristics of the organism. It was for some time supposed that the inheritance of certain embryonic characters was dependent on the cytoplasm rather than the nucleus; but it has been seen how these characters, although they develop in the first hybrid generation from an organization already present in the egg cytoplasm, show the Mendelian form of biparental heredity in subsequent generations. These cases are peculiar only in the delayed effect of the paternal nucleus. Some biologists incline to the view that all heredity is ultimately Mendelian. If this turns out to be true, then all heredity is probably dependent primarily on nuclear factors.

On the other hand, those chlorophyll characters in plants which have been reviewed in the foregoing pages appear to involve a second type of heredity. While some such characters manifesting themselves in abnormal plastid and pigment development are clearly Mendelian, the inheritance of others seems to depend on something external to the nuclei. Since plastids are known to maintain a certain degree of genetic continuity by division, hypotheses based on plastid individuality have been used in this connection. But that this continuity extends throughout the life cycle, as such hypotheses require, is not known in the case of the plants under investigation; nor have those other hypotheses postulating a cytoplasmic disease affecting the plastids yet received adequate cytological verification. The final evaluation of such hypotheses must await a fuller knowledge of the cytoplasm and its many differentiations. The data at hand strongly suggest that the plastids themselves are not primarily responsible for the abnormalities in question, but rather that their peculiar behavior is a result of some less evident condition of the cytoplasm. It hardly seems likely that the cytoplasm and plastids are here exempt from non-hereditary influences of the nucleus. How it is that the nucleus may exert such an influence, without acting in its specific hereditary capacity as in the Mendelian chlorophyll types, is a problem awaiting solution.

We would again emphasize the fact that, whatever the form in which the factors of organic inheritance are transmitted, the characters dependent on them are brought to expression through the action of the protoplasmic system as a whole. The nuclear theory of heredity does not assume the organism's characters to be due exclusively to the nucleus, but only that the protoplasmic reactions resulting in these characters are affected in a peculiar differential manner by nuclear factors. They are also influenced, though probably not in the same manner, by factors located elsewhere or pervading the whole protoplast, and by environmental factors as well. The general character of an organism is the result of reactions in the system, *organism-environment*, but the kinds of reactions which occur seem to depend in a peculiar way upon the genetic factors, which are transmitted largely, if not wholly, by the nucleus.

# CHAPTER XIX

## SEX

The modern scientific interest in the problem of sex is by no means prompted wholly by practical considerations. The great bulk of recent research has been done not merely for the sake of practical benefits which knowledge in this field might confer, but mainly in the hope that it may lead to an understanding of the origin, nature, and biological significance of sex itself, and to a solution of some of the problems of heredity. For this reason studies have not been confined to man and his economically important animals. Any animal or plant, no matter how obscure, that gives promise of yielding evidence is exhaustively investigated; and there can be no doubt that knowledge gained from such studies will, if sound, be directly applicable to practical ends.

During the closing decades of the nineteenth century many researches were carried out in the hope of identifying the controlling agency in sex-determination with one or more of the environmental factors. The effects of light, temperature, moisture, and nutrition were examined, and although a number of workers believed their methods to be in a certain measure successful, the results were on the whole inconclusive. Among all the ideas put forward the most suggestive, in view of what has more recently been ascertained, was that of Geddes and Thomson (1889), namely, that the two sexes differ primarily in the character of their metabolism, the female sex being characterized by the preponderance of anabolic processes and the male sex by those essentially katabolic in nature. This conception is important not only in connection with the question of sex control, but chiefly with respect to the more fundamental problem of the nature of sex itself.

The long period during which sex was looked upon as a character more or less under the control of the environmental factors was succeeded by one in which it came to be regarded as something automatically regulated by some internal mechanism or condition, and as relatively unalterable by external agencies. This conclusion, definitely reached by Cuénot (1899) for animals and by Strasburger (1900*c*) for plants, received the support of a number of experimental researches on animals and diœcious plants; and it was further strengthened by the discovery that in many organisms males and females differ visibly in their chromosome complements, these differences having their origin in the processes of meiosis and syngamy, where there was already much evidence to show that factors for other characters segregate and aggregate.

At the present time, therefore, biologists are separated into two rather well-defined schools, the one holding that sex-determination is most closely correlated with the operation of the nuclear mechanism thought to be largely responsible for the inheritance and development of Mendelian characters, and the other holding it to be chiefly the result of the influence of environmental factors upon the metabolism or physiological state of the organism. In this chapter will be reviewed some of the data upon which these two opinions are based, after which the question of their reconciliation will be considered.

## PLANTS

Attention must first be directed to the variety of sexual conditions found among plants, and to the terms by which they should be designated (see Fig. 188). *Homothallic* plants are those manifesting the two sexes in the same gametophyte, or thallus; *heterothallic* plants are those manifesting them in separate ones. *Heterophytic* plants are those in which two kinds of spores, with male and female tendencies respectively, are borne by separate sporophytes. *Homophytic* plants are those in which a single sporophyte bears two kinds of spores, with male and female tendencies respectively, or spores of one kind with a bisexual tendency. Bryophytes, so far as known, are all homophytic, but they may be either homothallic or heterothallic. Seed plants, on the other hand, are all heterothallic, but they may be either homophytic or heterophytic.

Species with spores of two sizes (megaspores and microspores) are ordinarily said to exhibit "heterospory," and those with spores of one size "homospory." The feature of fundamental importance here, however, is not mere size, but rather the presence or absence of sexual differentiation among the spores, such a differentiation frequently being very pronounced where there is no size difference. One may therefore designate as *heterosporic* any species with spores of two kinds as regards sexual tendency, whether these are alike or unlike in size, and whether they are produced as members of the same quartet or in separate quartets. Species with spores of only one kind as regards sexual tendency are called *homosporic*. Species with spores of one kind, and species bearing two kinds of spores in one sporangium, are *homosporangic;* species bearing the two kinds of spores in separate sporangia are *heterosporangic*.

The foregoing terminology was introduced by Blakeslee (1906). Two additional terms, *disporic* and *digametic*, are of service in dealing with seed plants with two kinds of microspores, male gametophytes, and male gametes.

**Fungi and Algæ.**—In the fungi there is considerable evidence indicating that sexual tendencies are bound up with a mechanism functioning at the time of spore formation. It was found by Blakeslee (1906) that in

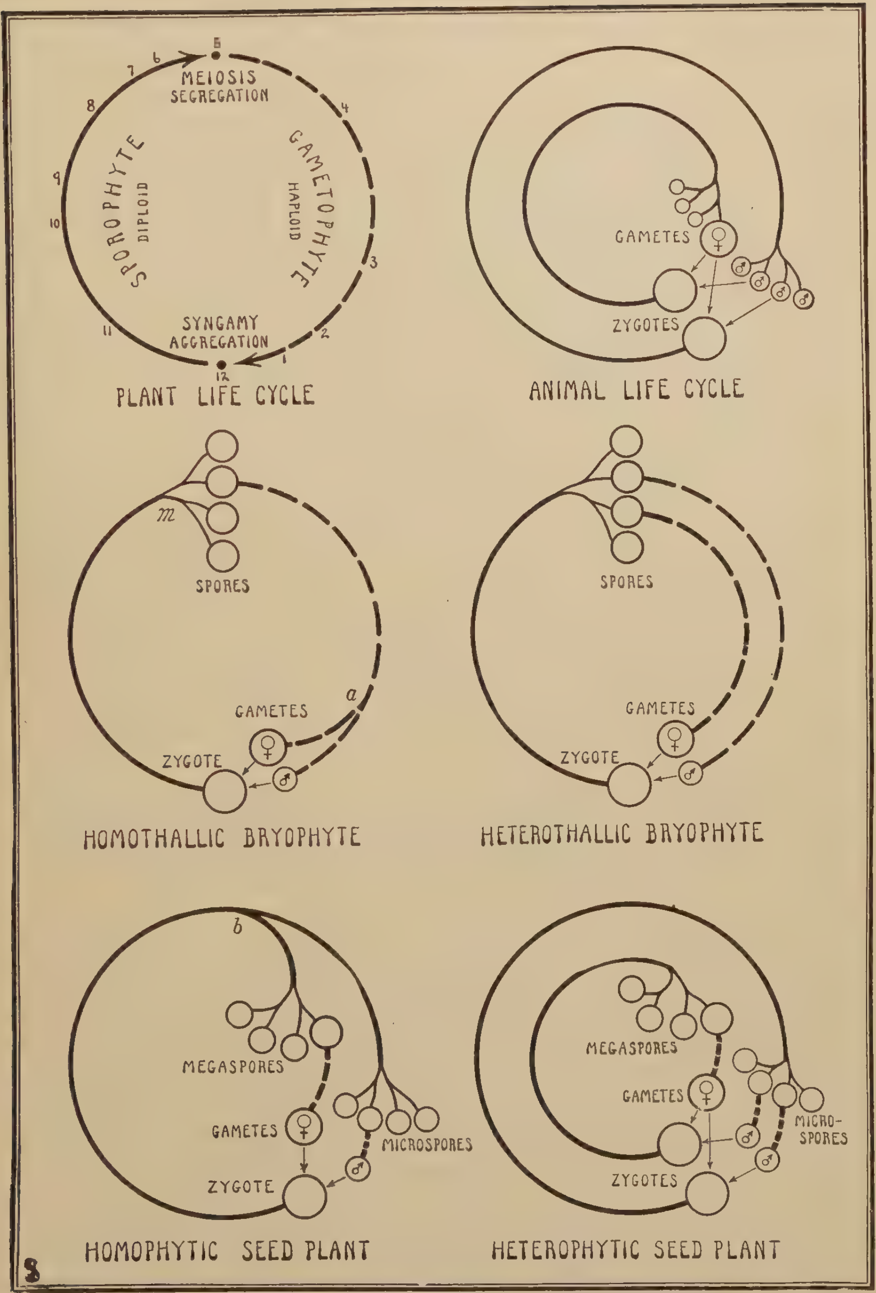

FIG. 188.—Diagrams of life cycles of several types. Explanation in the text. The first diagram is a modification of one by Schaffner (1923*c*). (*After Sharp*, 1925.)

certain strains of a mold, *Phycomyces nitens*, the spores produced in the germ sporangium are of three kinds as regards sexual tendency: "plus" "minus," and "neutral." Only the plus and minus mycelia are capable of sexual interaction, and either will perpetuate its characteristic condition indefinitely by asexual reproduction. It was suggested by Burgeff (1913, 1914, 1915) that it is primarily the nuclei which differ in such cases: the spores have one or more nuclei, and the tendency of any given spore or mycelium depends upon the relative number of its plus and minus nuclei. Burgeff was able to prove this by introducing the protoplasm of one sporangiophore into the sporangiophore of the opposite sex, whereupon the resulting sporangium produced spores of all three sexual types. Certain investigators have begun an analysis of the physiological differences correlated with the sexual states in these phycomycetes (Blakeslee, 1920*b*; Dunn, 1921).[1]

Heterothallism has also been demonstrated in basidiomycetes, notably in the hymenomycetous genera *Coprinus*, *Aleurodiscus*, *Panæolus*, and *Schizophyllum*.[2] In certain species it has been found that when a mycelium is grown from a single spore, the carpophores, if formed at all, continue to produce spores of the same sexual type (*cf.* p. 326). If mycelia from spores of different sexual strains are mingled, unions occurring between them result in mycelia with binucleate cells; and when basidia are formed by carpophores arising from such mycelia, two spores of the quartet borne by each basidium after nuclear fusion and meiosis differ regularly from the other two in sexual tendency, as shown by the behavior of the mycelia they produce. The peculiar results obtained in certain genera are thought by some investigators (Kniep, Hanna) to indicate the presence of two pairs of sex factors, which make possible four types of spores and mycelia. In *Ustilago*, as in the hymenomycetes, there is evidently a segregation of sex factors in the mitoses which differentiate the nuclei of the basidiospores (Kniep, 1919).

The experiments of Klebs have shown that in many green algæ the environmental conditions very largely determine whether the plants shall grow vegetatively, produce zoöspores, or reproduce sexually. The factors influencing the kind of sex produced, however, have been very little investigated in the algæ. A great many forms are homothallic. In *Vaucheria* it has even been shown that bisexual plants may be formed by regeneration from the contents of either the antheridium or the oögonium, which indicates that any internal sex factors here are not sharply segregated in gametogenesis (von Wettstein, 1920). In certain red algæ, such as *Polysiphonia*, the development of distinct male and female plants from the tetraspores suggests a segregation of sex factors in sporogenesis, but that such a segregation occurs within each quartet has not yet been directly demonstrated.

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[1] A review of researches on heterothallism in fungi is given by Cutting (1921).

[2] Kniep (1915–1923), Bensaude (1918), Vandendries (1923*ab*, 1924, 1925*ab*), Mounce (1921, 1922), Hanna (1925).

**Bryophytes.**—The usual statement regarding sex-determination in homothallic bryophytes (and ferns) is that made by Strasburger (1910*a*), namely, that the "sexes are separated" in the vegetative divisions at the time the sex organs are formed. This conclusion seemed to be borne out by results of certain experiments with a homothallic moss, *Funaria hygrometrica*, in which tissue taken from near the antheridia tended to produce only antheridial plants by regeneration (E. J. Collins, 1919). Correns (1920*c*), however, using the same species, obtained both antheridia and archegonia on gametophytes produced by regeneration from wall cells of the antheridium, as well as on those from wall cells of the archegonium. Since these cells are so closely related to the gamete-forming cells, Correns thinks it highly probable that the gametes themselves carry the potentialities of both sexes. In a further study, Collins (1925) also has found that the gametophytes produced by regeneration from tissue near the sex organs are bisexual. It therefore appears that there is no segregation of sex factors in the vegetative divisions preceding the formation of sex organs in such homothallic mosses.

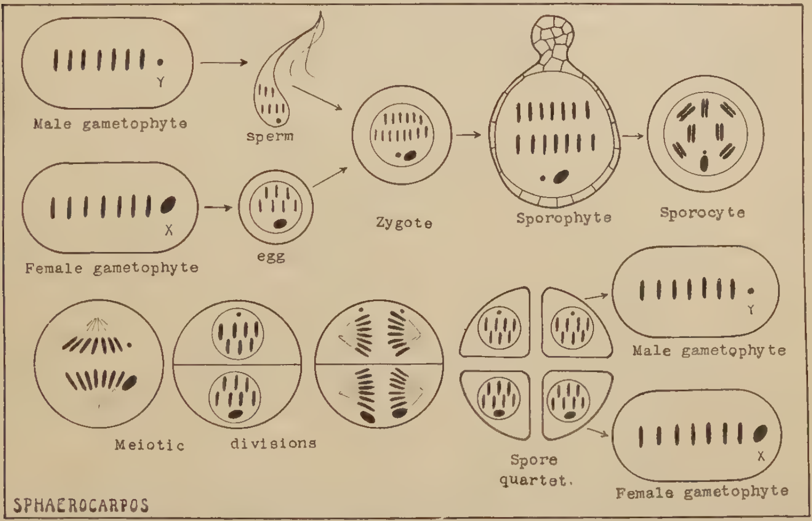

FIG. 189.—The history of the chromosomes in the life cycle of *Sphærocarpos*. (*Based on data of C. E. Allen*, 1917, 1919.)

In the heterothallic bryophytes there is found abundant evidence for the view that a definite segregation of sex factors of some kind occurs at the time of meiosis. The experiments of the Marchals (1906, 1907, 1909) afford a well-known case in point. In certain mosses these investigators found that two kinds of spores are produced in equal numbers in the capsule. These spores develop respectively into male and female gametophytes; such forms are therefore heterosporic and heterothallic. In no way were the Marchals able to alter the sexes of these gametophytes. New gametophytes formed from them by regeneration, moreover, were found to be similarly fixed as to sex. Gametophytes produced by regeneration from the tissue of the sporophyte, however, bore both antheridia and archegonia. It therefore appeared that both sex potentialities were present in the cells of the sporophyte and in those of the diploid gametophytes regenerated from it, whereas the normal haploid gametophytes developed from spores were either purely male or purely female.

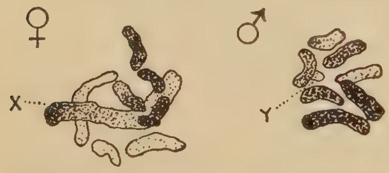

Fig. 190.—Chromosome sets from the female and male gametophytes of *Sphærocarpos Donnellii*. (*After C. E. Allen*, 1919).

Results similar to the above have been reported by Schweizer (1923) for *Splachnum sphæricum*. In two other genera Fleischer (1920) finds that the spores are of two sizes, the larger ones apparently giving rise to male plants, which are dwarfed. It has long been known that if the gametophytes of *Marchantia* are propagated repeatedly from gemmæ, the sex in any given line remains the same in spite of wide alterations in the environmental conditions (Noll; Blakeslee, 1906). The occasional appearance of androgynous receptacles in such heterothallic liverworts (Cutting, 1910) shows, however, that the segregation of sex factors here cannot be absolute.

Among bryophytes perhaps the most interesting case is that of *Sphærocarpos* (Figs. 189, 190). In this genus of heterothallic liverworts Douin (1909) and Strasburger (1909*b*) showed that two spores of a single quartet develop into male gametophytes and two into females. Some years later C. E. Allen (1917, 1919) discovered in *S. Donnellii* the first "sex-chromosomes" known in plants. The sporophyte has eight pairs of chromosomes, including a very unequal "*XY*" pair. At the time of sporogenesis the *X* and *Y* separate in the first mitosis and divide longitudinally in the second. The two spores receiving an *X*-chromosome develop into female gametophytes, while those receiving a *Y*-chromosome develop into males. The same situation is present in *S. texanus* (Schacke, 1919).

The obvious conclusion to be drawn from the phenomena observed in heterothallic bryophytes is that a differential segregation of sex factors of some kind takes place during the meiotic divisions. In some cases the spores of the quartet are visibly alike, but of two kinds functionally; in others two of the spores differ in size from the other two, and in *Sphærocarpos* the male-producing and female-producing spores differ conspicuously in their chromosome complements.

**Pteridophytes.**—The gametophytes of ferns are probably more often homothallic than heterothallic, but the dependence of these states upon environmental conditions in some degree has often been demonstrated. In *Osmunda* and *Asplenium*, which are homothallic under ordinary conditions, Nagai (1914, 1915) found that the concentration of the Knop's solution used had a marked effect upon the kind of sex organs produced. In *Onoclea*, which is ordinarily heterothallic, Wuist (1913) was able to make the female gametophytes bisexual by growing them under certain conditions, but the males proved to be more refractory. Czaja (1921) finds that the several species whose sex relations he investigated fall into two general classes. Those of the first class are bisexual under normal conditions, male under poor nutritive conditions, and female very seldom. Those of the second class are female under normal conditions, bisexual under poor nutritive conditions, and male only when the sowing is dense. He further finds that filamentous structures regenerated from the basal cells of the archegonia and antheridia can be made to exhibit both sexes, although this is difficult in the case of those derived from antheridial cells. Thus the "separation of the sexes," which Strasburger (1910) supposed occurred at the time of sex organ formation, cannot be absolute. Czaja (1924) is of the opinion that in all homosporous ferns so far studied, heterothallism is only facultative.

Such results as these, taken together with the fact that so many bryophytes and pteridophytes have bisexual gametophytes (*i.e.*, are homothallic), serve to show that haploid as well as diploid tissues may possess the potentialities of both sexes. This appears to be true even of gamete nuclei. In meiosis in different plants there are probably all intergrades between an equational distribution of factors influencing the production of the two sexual states, which results in homothallism, and a highly differential distribution, which is correlated with heterothallism.

**Angiosperms.**—With regard to homophytic (monœcious and hermaphroditic) angiosperms, botanists in general have followed Strasburger in holding that the "sexes are separated" in the sporophyte at some stage prior to the development of microspores and megaspores.[1] They have also long been aware of the variations in sexual expression occurring under different environmental conditions, a matter which will be dealt with further on.

For many years evidence has been accumulating to show that the heterophytic (diœcious) condition in seed plants is in some way connected with a qualitative difference among the pollen grains, *i.e.*, that such plants are disporic. Correns (1907) was led to this conclusion by the results of his experiments on *Bryonia* hybrids. He was best able to interpret these results on the hypothesis that the eggs are all similar in having a female sex "tendency;" that there are two kinds of microspores and hence two kinds of male gametes, with male and female tendencies respectively; and that the male tendency dominates the female, so that half of the sporophytes bear microspores and half megaspores. In such cases Strasburger (1910*a*) assumed that the tendency of all the pollen grains, and hence male gametes, is toward maleness: some have a "strong" male tendency which dominates the female tendency of the egg, staminate plants being so produced, while others have a "weak" male tendency which is dominated by the female tendency of the egg, carpellate individuals so resulting.

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[1] With regard to the use of terms implying sexuality in connection with the sporophyte, see the discussion by Sharp (1925).

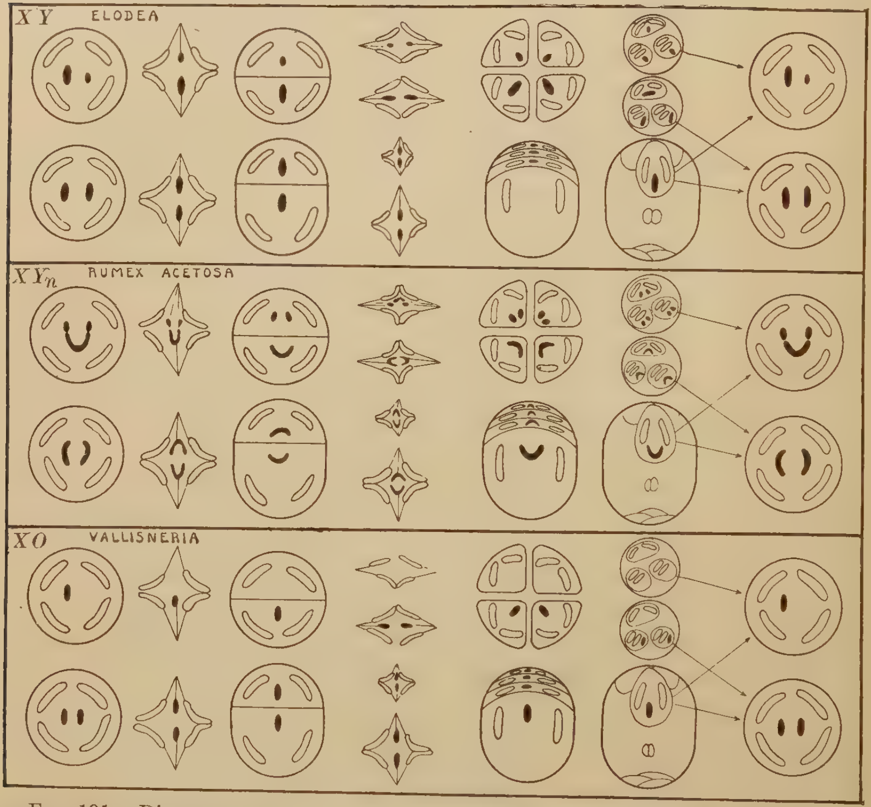

FIG. 191.—Diagrams showing the distribution of sex-chromosomes (black) of three general types throughout the life cycle in angiosperms. In each diagram the upper row represents the staminate plant, and the lower row the carpellate plant. In the carpellate plants the chromosome behavior is at present known for *Elodea*, but only inferred for *Rumex* and *Vallisneria*.

The view that the pollen grains are thus of two kinds, with a differential effect upon the sex of the offspring, received striking cytological confirmation in six species of heterophytic angiosperms during 1923.

In *Elodea canadensis* the four pollen grains of each quartet cling together when shed. At the time of his death in 1912 Strasburger was engaged upon a study of the sexual tendencies of these grains. He pollinated many stigmas with single quartets, but did not live to see the results. Santos (1923, 1924) has made a cytological investigation of this species, and reports that two of the grains differ from the other two in

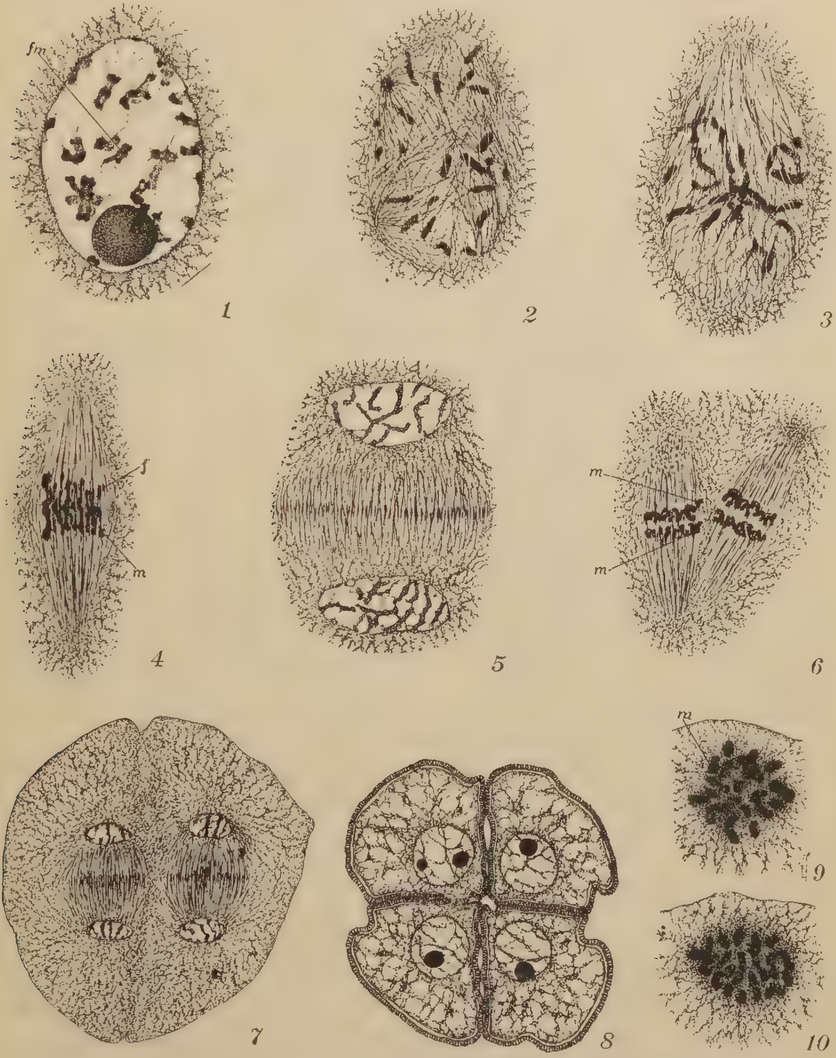

FIG. 192.—Chromosome behavior in the microsporogenesis of *Elodea canadensis*. *1*, diakinesis, showing unequal chromosome pair *fm* (*XY*). *2,3*, development of achromatic figure in nuclear area. *4*, beginning of the anaphase of *I*; *f* and *m* disjoining. *5*, telophase of *I*. *6*, anaphase of *II*; *m*-chromosomes in one figure; *f*-chromosomes indistinguishable from other chromosomes in other figure. *7*, telophase of *II*; two nuclei smaller than other two. *8*, microspore quartet. *9*, metaphase of mitosis in microspore with *m*-chromosome. *10*, metaphase in microspore with *f*-chromosome. (*After Santos*, 1924.)

their chromosome complements (Figs. 191, 192). The somatic nuclei contain 48 chromosomes. At diakinesis in the microsporocytes there are 24 pairs, including an unequal *XY* pair. All of the pairs disjoin in the first division, and the second division is equational, so that half of the microspores (and hence male gametes) receive a *Y*-chromosome and 23 other chromosomes ("autosomes"), while the other half receive 23 autosomes and an *X*-chromosome. In the nuclei of the carpellate plant there are two *X*-chromosomes, every egg receiving one of them. It is therefore evident that the union of an egg with a male gamete carrying a *Y*-chromosome results in the production of a staminate plant, while a union with a male gamete with an *X*-chromosome leads to the production of a carpellate plant. This is the first known case of sex-chromosomes among the vascular plants.

The genus *Melandrium* (*Lychnis*) has long been a favorite group for studies on sex. Strasburger (1910*a*) was convinced that there must be two kinds of pollen grains here, and G. H. Shull (1910, 1911) showed experimentally that in *Lychnis dioica* the staminate plant is heterozygous for sex. In seeking an explanation for the preponderance of carpellate plants in this genus, Correns (1918*b*, 1920*b*, 1921, 1922) found that the pollen tubes formed by "female-producing" grains grow more rapidly than those of the "male-producing" grains, and thus reach a larger proportion of the ovules. When relatively small amounts of pollen are used, thus lessening the competition unfavorable to the male-producing pollen, the ratio of staminate and pistillate plants among the offspring is changed decidedly toward equality. Sex-chromosomes in *Melandrium album* have been described independently by Blackburn (1923), Winge (1923*b*) and Heitz (1925*b*) (Fig. 193, *C*). These investigators report the presence of an unequal *XY* pair in the staminate plant, the members of the pair disjoining in the first division in the microsporocytes; and Blackburn finds an equal pair in the carpellate plant. Blackburn (1924) reports the same condition in *Lychnis dioica* and *L. alba* × *dioica*, and concludes that the larger member of the unequal pair is the *Y*.

In *Rumex acetosa* Correns (1922*b*) finds that the staminate plant is disporic, and that there is a considerable difference in the rapidity with which the pollen tubes carrying male-determining and female-determining gametes grow downward through the styles. Kihara and Ono (1923) report a peculiar sex-chromosome condition in this species (Fig. 191). In the staminate plant the somatic number appears to be 15. In the microsporocytes there are six gemini and one triple group composed of a large member (*M*) with a small member attached to each of its ends ($m_1$ and $m_2$). In the first meiotic division *M* disjoins from $m_1$ and $m_2$, and in the second division all of the chromosomes split longitudinally; hence two of the microspores receive seven chromosomes (6 autosomes + *M*), while the other two receive eight (6 autosomes + $m_1$ + $m_2$). The somatic nuclei of the carpellate plant contain twelve autosomes and two $M$-chromosomes. It thus appears that fertilization by a male gamete with $M$ results in a carpellate plant, and that by a gamete with $m_1m_2$ in a staminate plant. Kihara and Ono regard the $M$-chromosome as an $X$, and the $m_1$ and $m_2$ elements as a $Y$-complex; hence one may term this the "$XY_n$ type." The same behavior is observed in *R. thyrsiflorus* by Meurman (1925), but in *R. acetosella* this author reports that the $M$ and one $m$ disjoin from the other $m$ in the first meiotic division (Fig. 193, *G*).

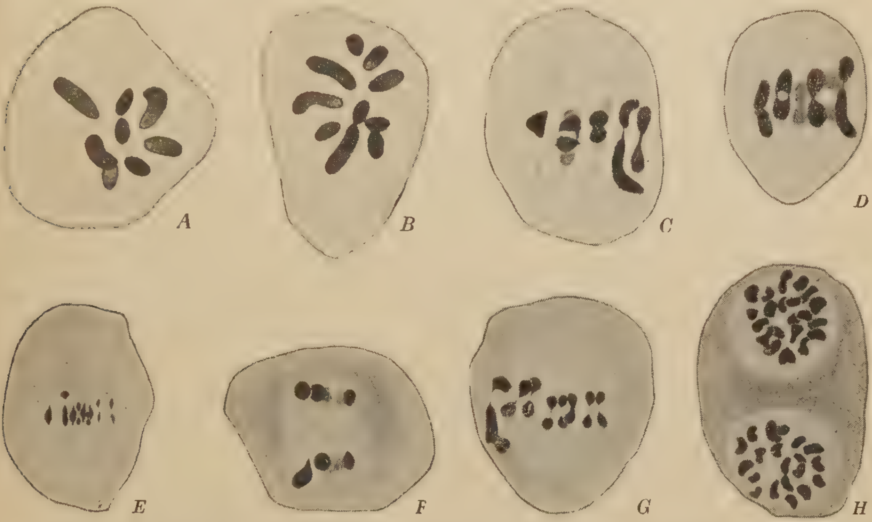

Fig. 193.—Sex-chromosomes in heterophytic angiosperms. *A*, division of microspore nucleus in *Vallisneria spiralis*, showing 8 autosomes. *B*, division of another microspore of the same, showing 8 autosomes and a long constricted $X$-chromosome. *C*, meiotic division *I* in *Melandrium album*, showing $XY$ pair about to disjoin. *D*, division *I* in *Humulus japonicus*, showing $XY$ pair at right. *E*, *Populus balsamifera*, with $XY$ pair. *F*, *Valeriana dioica*, showing $X$ and $Y$ disjoining in division *I*. *G*, *Rumex acetosella*, showing $Mm$ disjoining from $m$ in division *I*. *H*, polar view of division *II* in the same, showing 21 chromosomes in one figure and 20 in the other. (*A–D after Winge*, 1923*b*; *E–H after Meurman*, 1925.)

Sex chromosomes of the $XY$ type are also found in the genus *Humulus* (Winge, 1923) (Fig. 193, *D*). In both *H. lupulus* and *H. japonicus* the somatic chromosome number in the staminate plant is 20, including an unequal $XY$ pair whose members disjoin in meiosis. The larger member is constricted, and is assumed to be the $X$. It seems that in *Humulus*, as in the cases mentioned above, the preponderance of carpellate plants is the result of a more rapid growth on the part of the pollen tubes carrying female-producing gametes. Winge thinks it not improbable that this is due to their relatively greater amount of karyotin, and cites in support of this view the case of *Spinacia*, in which a numerical equality of staminate and carpellate plants among the offspring (Nohara, 1923) is correlated with an absence of any discernible difference in the chromosome complements of the microspores.

Following the statement of Blackburn and Harrison (1924*a*) that "there is some evidence of the existence of heterochromosomes in the male of both *Populus* and *Salix*," Meurman (1925) has found that the staminate plants of *Populus trichocarpa*, *P. balsamifera*, and *P. Simoni* all have an *XY* pair in addition to 36 autosomes (Fig. 193, *E*). *Valeriana dioica* has such a pair in addition to 14 autosomes. There is some evidence that *Urtica dioica* also belongs in the *XY* category.

Finally, in *Vallisneria spiralis* Winge (1923) has found an example of the "*XO* type" of sex-chromosome differentiation (Figs. 191; 193, *A*, *B*). The staminate plant has 17 chromosomes in its somatic nuclei. In the microsporocyte there are eight gemini, an unpaired element remaining as the *X*-chromosome. Since the *X*-chromosome passes to one pole in the first mitosis and divides equationally in the second, half of the microspores receive nine chromosomes (8 + *X*) and half receive only eight. It is presumed that the carpellate plant will show 18 chromosomes, including two *X*s. It is of interest to note that *Vallisneria* and *Elodea* belong to the same family, the Hydrocharitaceæ. According to Meurman (1925), a second example of the *XO* type has probably been found in *Dioscorea sinuata*.

The foregoing cases are sufficient to show clearly that in a considerable number of angiosperms there is an internal mechanism whose operation is definitely correlated with the expression of the sexes. Reference must now be made to researches showing the pronounced effect which various external factors may have upon the sexual characters in this group.

Field taxonomists and experimental workers are well acquainted with the frequent intergrades between the purely staminate and purely carpellate conditions in normally heterophytic flowering plants, and with the changes in sex expression which may be induced in both heterophytic and homophytic forms by appropriate alterations in the environmental conditions. The work of Schaffner (1919–1925) in this field is particularly well-known. The effects of age, nutrition, length of day, and other factors have been investigated and shown to be very marked in a number of plants, including *Cannabis sativa*, *Morus alba*, *Salix amygdaloides*, *Humulus japonica*, *Thalictrum dasycarpum*, and *Arisœma Dracontium*. In *Cannabis*, for example, staminate and carpellate individuals are found in equal numbers in the open in spring. In the greenhouse in winter, however, all sorts of intermediates appear; and both staminate and carpellate plants may undergo sex-reversal during the growth period. It has furthermore been found that when the days are long the plants tend to be purely unisexual, whereas a shortening of the light period is accompanied by sex-reversals in both directions and in various degrees. In *Arisœma* "dichotomous twins" are normally of the same sex, but they may be made unlike in sex by placing them under different cultural conditions. Observations on the variation of sex manifestation in angiosperms have also been made on *Myrica Gale* by Davey and Gibson (1917), on *Plantago lanceolata* by Bartlett (1911), Correns (1908), and Stout (1919), and on *Mercurialis annua* by Yampolsky (1919, 1920).

It is, of course, understood that the influence of such external conditions upon expressed characters is not exerted directly, but through the intermediary of altered metabolic processes. Stout (1923) emphasizes the determining rôle of periodically recurring internal physiological states in his work on *Cleome spinosa*. He holds that "the morphological differentiations of sex are fundamentally an extension of the phenomena of somatic differentiations," and that the "sex of flowers is determined progressively as they are formed in response to regulation by internal biogenetic conditions."

From the foregoing review it seems clear that the sexual manifestations of plants are under the influence of both intrinsic and extrinsic factors, which differ considerably in their respective controlling effects in different species. Discussion of this matter will be deferred until after the situation in animals has been reviewed.

## ANIMALS

In the higher animals the two sexes are normally separate. The male individual produces quartets of spermatozoa, while the female produces quartets of cells, of which one is the egg and the other three functionless polar bodies. In the production of these quartets meiosis occurs, as it does in sporogenesis in plants. The gametes unite to produce zygotes which develop into the individuals of the next generation. Although the heterophytic seed plant cycle includes spores and a much abbreviated haploid gametophytic phase, it is still strikingly similar to that of the animal, and for practical purposes in genetic investigation the two may be treated in essentially the same manner (see Fig. 188). The reason for the approximate numerical equality of males and females is to be sought in the gametes. In a large number of species the gametes of one sex (more commonly the male) have been found to be of two kinds, which frequently differ strikingly in their chromosome complements.

**Chromosomes and Sex.**—It was in animals that an intimate association of sex with specialized chromosomes was first discovered. In an insect, *Pyrrhocoris apterus*, Henking (1891) noticed that half of the spermatids contained a body which he thought might be a nucleolus. It was subsequently shown in a number of other insects by McClung (1899), Paulmier (1899), Montgomery (1901), and de Sinéty (1901) that this body was not a nucleolus but an extra or "accessory chromosome" (McClung), and that half of the spermatozoa actually differed from the other half in their chromosome complements. Henking's misinterpretation had apparently been due to the fact that the accessory chromosome often remains very compact while the other chromosomes become diffused or reticulate in form, and often exhibits other peculiarities of behavior. It was at once suggested by McClung (1901, 1902) that the accessory chromosome in some way determines sexual differentiation, *i.e.* that eggs fertilized by one kind of spermatozoön develop into females, while those fertilized by the other kind become males. This represents the first attempt to associate a given character with a particular chromosome. An extensive series of researches was now begun by McClung, Payne, E. B. Wilson, N. M. Stevens, and a number of other cytologists, who discovered several types of sex-chromosomes, not only among the insects, where they are best displayed, but also in certain echinoderms, mollusks, nematodes, and vertebrates, including birds and man. In the majority of known cases, including mammals and most insects, it is the male which is "digametic," or "heterogametic," but in some groups, notably birds and Lepidoptera, the female is digametic. It has further been found that the differential disjunction of sex-chromosomes responsible for the digametic condition occurs in most groups in the first meiotic mitosis, but in other cases, notably in the Hemiptera heteroptera, it occurs in the second.[1]

*Male Digametic.*—The condition originally observed by Henking, in which half of the spermatozoa carry one sex-chromosome (*X*) and the other half none—the so-called "*XO* type"—has been found in a number of animals. In *Protenor belfragei*, a bug, the situation is as follows (Montgomery, 1901; Wilson, 1906; Morrill, 1910) (Figs. 194; 195, *C*, *D*).[2] In the male somatic nuclei and the spermatogonia there are six pairs of autosomes and a single unpaired *X*-chromosome. The autosomes undergo disjunction in *I* as usual and divide equationally in *II*, but the *X*-chromosome divides in *I* and passes undivided to one pole in *II*.[3] Two sperms of the quartet receive one *X* each, while the other two receive none. In the female somatic cells and the oöcytes there are two *X*-chromosomes besides the autosomes; every egg receives one. Fertilization by a spermatozoön with an *X* results in a female with two *X*s, whereas that by one with no *X* results in a male with only one. In a

[1] See the reviews by Payne (1909), Wilson (1911), Agar (1920), Doncaster (1920), and especially the discussion by Wilson (1925).

[2] For the sake of clearness the diploid number of autosomes in all of these diagrams is arbitrarily shown as four. The sex-chromosomes in the female are represented as disjoining at the same mitosis as in the male, but in most cases this has not been demonstrated.

[3] The mitosis in which the *X* passes undivided to one pole has been called *heterokinesis* by Gutherz (1907). Both preheterokinesis (in *I*) and postheterokinesis (in *II*) occur, even in the same genus; and a tendency to lag on the part of the *X* may result in the occurrence of both modes in the same species (Edwards, 1910, on *Ascaris*) (see Wilson, 1925, p. 755).

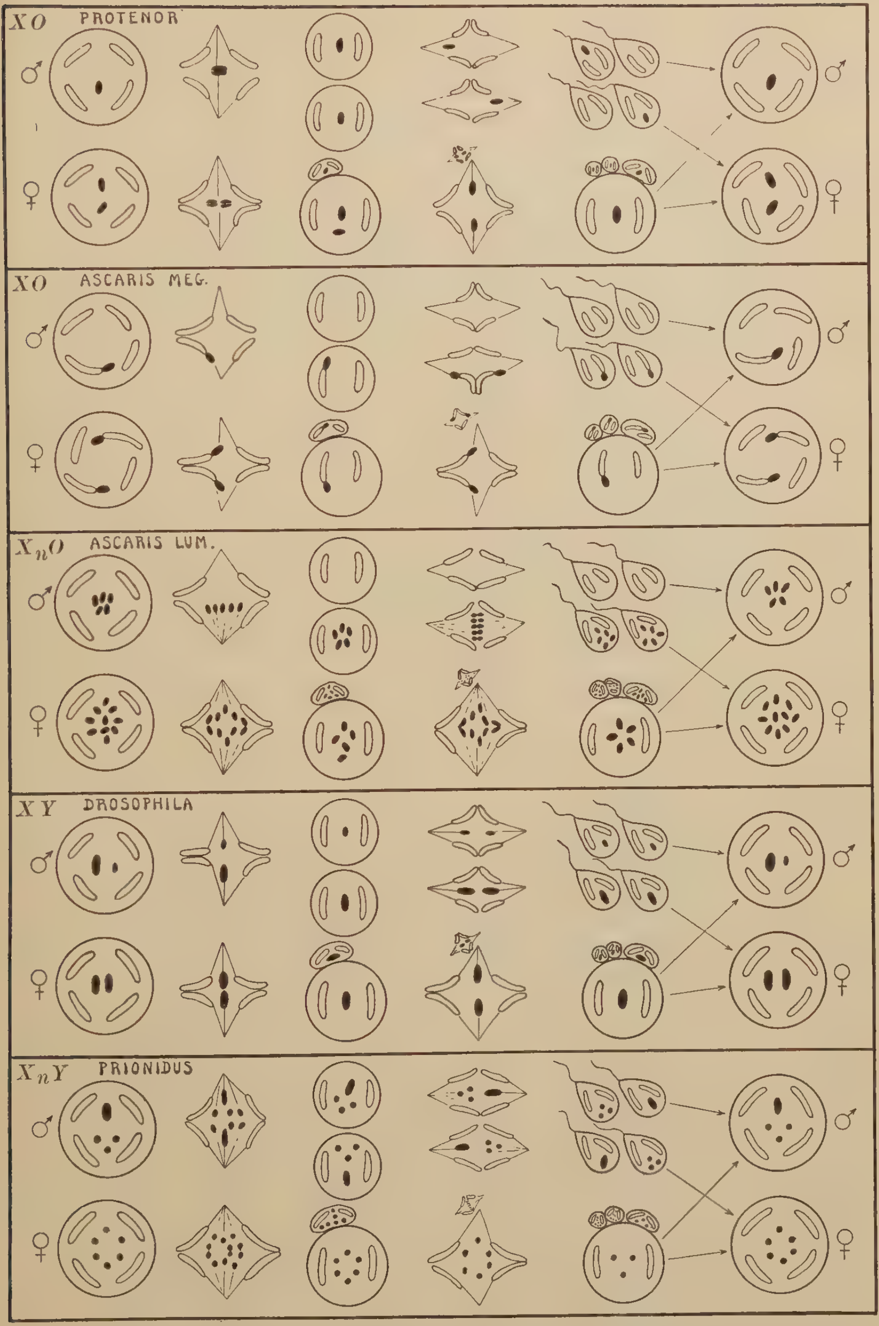

FIG. 194.—Diagrams showing several types of sex-chromosome behavior in animals with digametic males. In each case the sex-chromosomes in the female are shown disjoining in the same mitosis as in the male, though this is not certainly known to occur in *Protenor* and *Prionidus*. In *Drosophila* the *X* and *Y* are about alike in size, but in many animals the *Y* is much the smaller.

number of insects, domesticated mammals,[1] and lizards (Painter, 1920, 1921*b*) the *X*-chromosome passes undivided to one pole in *I* and divides in *II*, the end result being the same as in *Protenor*. Malone has shown that plotted measurements of the spermatozoa of the dog form a bimodal curve, which indicates a size dimorphism associated with the chromosome difference. The *XO* type is also known in certain nematodes (Gulick, 1911; Mulsow, 1912).

Two interesting variants of the *XO* type are found in the nematode genus, *Ascaris*. In *A. megalocephala bivalens* (Fig. 194) there are in the spermatocyte four autosomes and a single small *X*, which is usually attached to the end of one of the autosomes.[2] The *X* passes undivided to one pole in *I* and divides in *II*, and hence is present in half of the spermatozoa. In the oöcyte there are two such *X*-chromosomes, which disjoin in *I* and divide in *II*, every egg thus receiving one. Fertilizations of the eggs by sperms with and without an *X* result in females and males respectively.[3] In *A. felis* Boveri (1911) and Walton (1921) report the same condition in the male, though the number of autosomes in this species is nine. The second variant is seen in *A. lumbricoides*, which has in the male an *X*-complex made up of five elements (Fig. 194). All five pass to one pole in *I*, and two classes of spermatozoa are formed, with 19 and 24 chromosomes respectively (Edwards, 1911). This is sometimes referred to as the "$X_nO$ type." In an insect, *Syromastes*, the *X*-complex consists of two elements (Wilson, 1909).

A considerable number of examples of the "*XY* type" of sex-chromosome differentiation have been described, chiefly in insects and mammals, including monkeys and man. In the opossum, *Didelphys virginiana*, the somatic number of chromosomes is 22, including a pair of sex-chromosomes: *XY* in the male and *XX* in the female. In the spermatocyte the *X* and *Y* disjoin in *I* and divide in *II*, giving two spermatozoa with *X* and two with *Y* (Painter, 1921*a*, 1922*b*) (Fig. 196, *D*). Essentially the same condition, except for the number of autosomes, holds in five other genera of marsupials (Agar, 1923; Greenwood, 1923). In monkeys also an *XY* pair disjoins in *I* in the spermatocytes (Painter, 1922*a*, 1923*b*). In a new-world monkey the diploid number of chromosomes is 54, including the unequal *XY* pair. In *Rhesus maccacus*, an old-world species, the number is 48, as in man. Certain insects, including *Drosophila*, exhibit the *XY* type. In *D. melanogaster* there are normally four pairs of chromosomes, including two pairs of large bent autosomes, one pair of very minute autosomes, and one rod-shaped pair of sex-chromosomes: *XY* in the male and $XX$ in the female (Fig. 194). As in other organisms with the $XY$ type, fertilization by an $X$ sperm results in a female with $XX$, and that by a $Y$ sperm in a male with $XY$ (Stevens, 1907; Morgan, 1911; Metz, 1914). Experiments have made it evident that the male sex does not depend on the $Y$, but rather on the fact that there are fewer $X$-chromosomes than autosome pairs, as will be shown later. In a diploid fly, maleness and femaleness are correlated with the presence of one and two $X$-chromosomes respectively. Flies have been found with an $X$ and no $Y$, yet they are male; and females are known with $XXY$. In *Drosophila*

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[1] Malone (1918) on the dog; Wodsedalek (1913, 1914, 1920, 1922) on horses, sheep, pigs, and cattle; Masui (1919*ab*) on horses and cattle.

[2] Walton (1924) concludes from his extensive researches on nematodes that each autosome is here equivalent to 22 somatic chromosomes, and that the *X* is equivalent to 8.

[3] Boveri (1909*b*), Boring (1909), Edwards (1911), Frolowa (1912).

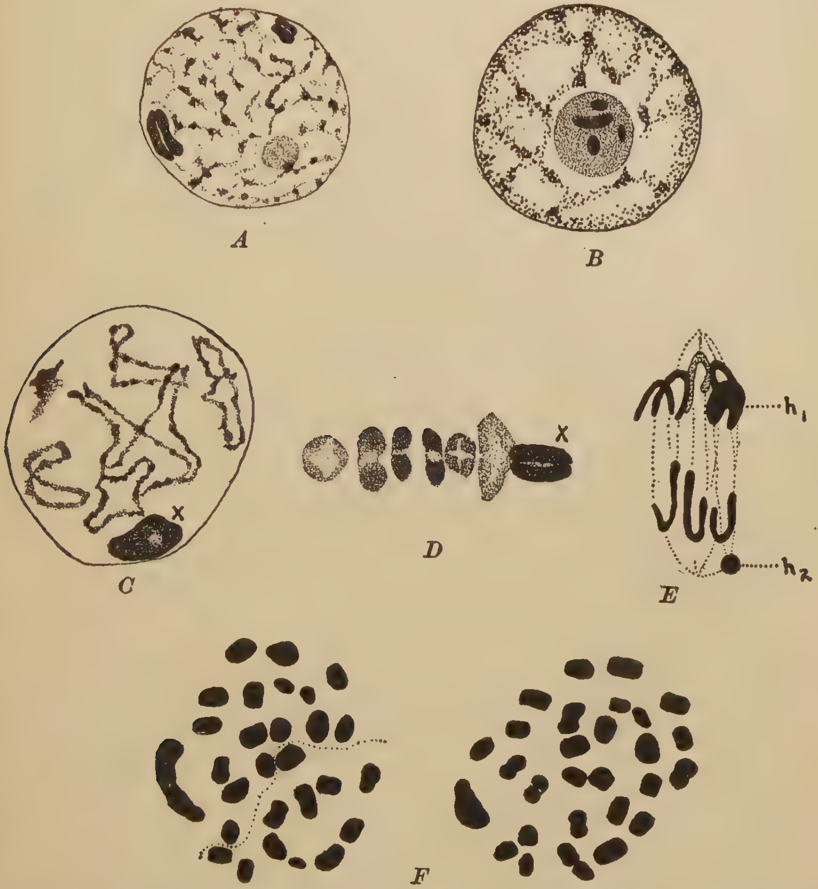

Fig. 195.—Sex-chromosomes in various insects. *A*, spermatocyte nucleus of *Lygæus*, showing *X*-chromosome at left and *Y*-chromosome above, both split. *B*, spermatocyte nucleus of *Prionidus*, showing sex-chromosomes enclosed in plasmosome. *C*, prophase in spermatocyte of *Protenor*. *D*, metaphase of division *I* in *Protenor*. *E*, anaphase of *I* in spermatocyte of *Musca domestica; h*, heterochromosomes. *F*, the two daughter chromosome groups in the anaphase of *I* in the oöcyte of *Phragmatobia fuliginosa*, showing 28–29 distribution. (*A*, *C*, and *D after E. B. Wilson; B after Payne; E after Stevens; F after Seiler.*)

*Willistoni* it has been shown by Lancefield and Metz (1921, 1922) that the sex-chromosomes are represented by one of the large bent pairs rather than the shorter rod-shaped pair; and there is evidence in the linkage relations of the genetic factors that the rod-shaped chromosome of *melanogaster* corresponds to one arm of the large bent sex-chromosome in *Willistoni* and *obscura*. In the insect genera, *Lygæus* and *Euschistus*, the *X* and *Y* are known to disjoin in *II*, rather than in *I* as in *Drosophila*. In certain additional cases in which the chromosomes have not yet been adequately studied the genetic evidence indicates the presence of an *XY* pair. This, for example, is true of the fish genera, *Lebistes* (J. Schmidt, 1920; Winge, 1922, 1923*a*) and *Aplocheilus* (Aida, 1922). There are probably many organisms with *XY* chromosomes not visibly differentiated from the other members of the complement.

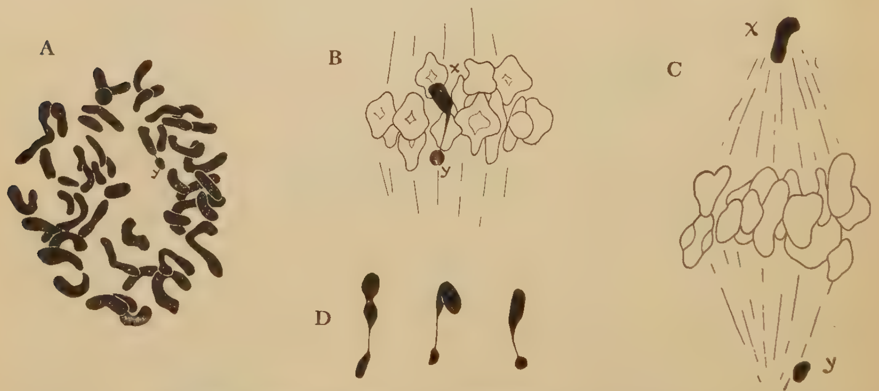

FIG. 196.—The chromosomes of man. *A*, diploid complement of 48 chromosomes in the male. *B*, metaphase of division *I* in spermatocyte, showing *XY* pair about to disjoin. *C*, the *X* and *Y* have disjoined and passed to the poles in advance of the autosomes. *D*, *XY* pairs in opossum, monkey, and man. (*After Painter*, 1923*a*, 1922*a*.)

The number of chromosomes in man and the make-up of the complement in the two sexes have long been subjects of controversy.[1] Several investigators reported about 12 pairs of chromosomes, but others (de Winiwarter, Evans, Painter, Oguma and Kihara) found twice as many. Intermediate numbers were also reported. The work of the above named authors appears to have shown conclusively that the correct number of pairs is 24, and that seemingly smaller numbers are due to a clumping of the chromosomes which often results from inadequate fixation. According to Painter, there are in both sexes 48 chromosomes, including an $XY$ pair in the male and an $XX$ pair in the female, precisely as in the old-world monkey. The $X$ and $Y$ disjoin at $I$ in the spermatocytes and presumably split at $II$, as in the opossum and other mammals mentioned in an earlier paragraph (Fig. 196). De Winiwarter and Oguma and Kihara fail to find the small $Y$-chromosome, and claim that the numbers in the male and female are 47 and 48 respectively ($XO$ type). The figures of Painter, however, leave no doubt concerning the presence of the $Y$-chromosome in his material.

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[1] Reports on the chromosomes of man have been made by more than 20 investigators, among whom may be mentioned Flemming (1882*b*, 1898), Moore and Arnold (1905), Duesberg (1906), Guyer (1910), Gutherz (1912), Montgomery (1912), de Winiwarter (1912, 1921*b*, 1921*a*), Wieman (1917), Evans (1918), Painter (1921*a*, 1922*a*, 1923*a*), Grosser (1921), Rappeport (1922), Oguma and Kihara (1922). See the résumés by de Winiwarter (1921*a*), Oguma and Kihara (1922), and Painter (1921*a*, 1923*a*).

As an example of the "$X_nY$ type" of sex-chromosomes may be cited the bug, *Prionidus*, described by Payne (1909) (Figs. 194; 195, *B*). Instead of a single $X$-chromosome, there are here three small elements which together behave as an $X$. In the male there are 11 pairs of autosomes, the three $X$-elements, and a $Y$. In spermatogenesis the $X$-elements disjoin from the $Y$ at $II$. There are six $X$-elements in the female somatic nuclei and three in the eggs. The two possible kinds of gametic union thus result in males with $X_3Y$ and females with $X_6$. In *Fitchia*, *Gelastocoris*, and *Acholla* the $X$-complexes are made up of two, four, and five elements respectively. In the earwig, *Anisolabis maritima* (Kornhauser, 1921), and the garter snake, *Thamnophis butleri* (L. Thatcher, 1922), a double $X$ is disjoined from a single $Y$ at $I$ in the spermatocyte.

It now seems probable that the $XO$ type has been derived from the $XY$ type through loss of the $Y$. In *Metapodius* the $Y$ may be either present or absent (Wilson, 1909), and it is not impossible that the same may be true of man.

*Female Digametic.*—In Lepidoptera and birds it has been found that the female, rather than the male, produces two kinds of gametes as regards the sex-chromosomes. Apparently both the $ZO$ and the $ZW$ types[1] are represented (Fig. 197).

The $ZO$ type is exemplified by the moth, *Talæporia tubulosa* (Seiler, 1917). In the female there are 59 chromosomes, including an unpaired $Z$. In some oöcytes the $Z$ passes to the first polar body at $I$, while in others it remains in the secondary oöcyte nucleus. All of the chromosomes appear to divide in $II$. Hence there are two classes of eggs, with 29 and 30 chromosomes respectively. In the male there are 60 chromosomes, including a $ZZ$ pair, and all of the spermatozoa are alike in having one $Z$. Fertilization of the two kinds of eggs would therefore be expected to give $ZO$ (♀) and $ZZ$ (♂). Seiler finds a similar situation in *Fumea casta*, the two classes of eggs in this species having 30 and 31 chromosomes respectively.

In another moth, *Phragmatobia fuliginosa*, Seiler (1913) has described an example of the $ZW$ type, though it is somewhat complicated by a tendency on the part of the *W*, and possibly also the *Z*, to undergo temporary fragmentation at certain stages. In the male the somatic number is 56, including 54 autosomes and 2 *Z*-chromosomes. Each sperm receives 28 (27 + *Z*). In the female the somatic number is likewise 56, but includes a *ZW* pair instead of the *ZZ* pair of the male. Half the eggs receive 27 + *Z* and the other half 27 + *Ww* (the *W*-chromosome breaks temporarily into two parts) (Fig. 195, *F*). An egg with 28 (27 + *Z*) fertilized by a sperm with 28 (27 + *Z*) develops into a male moth with 56 (54 + *ZZ*). An egg with 29 (27 + *Ww*) fertilized by a sperm with 28(27 + *Z*) develops into a female moth with 57 (54 + *ZWw*). The *W* and *w* subsequently reunite to form a single *W*, both sexes then having the same number, 56.

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[1] In digametic females it is customary to refer to the sex-chromosomes as $Z$ and $W$ rather than $X$ and $Y$, but this is not always done in the literature.

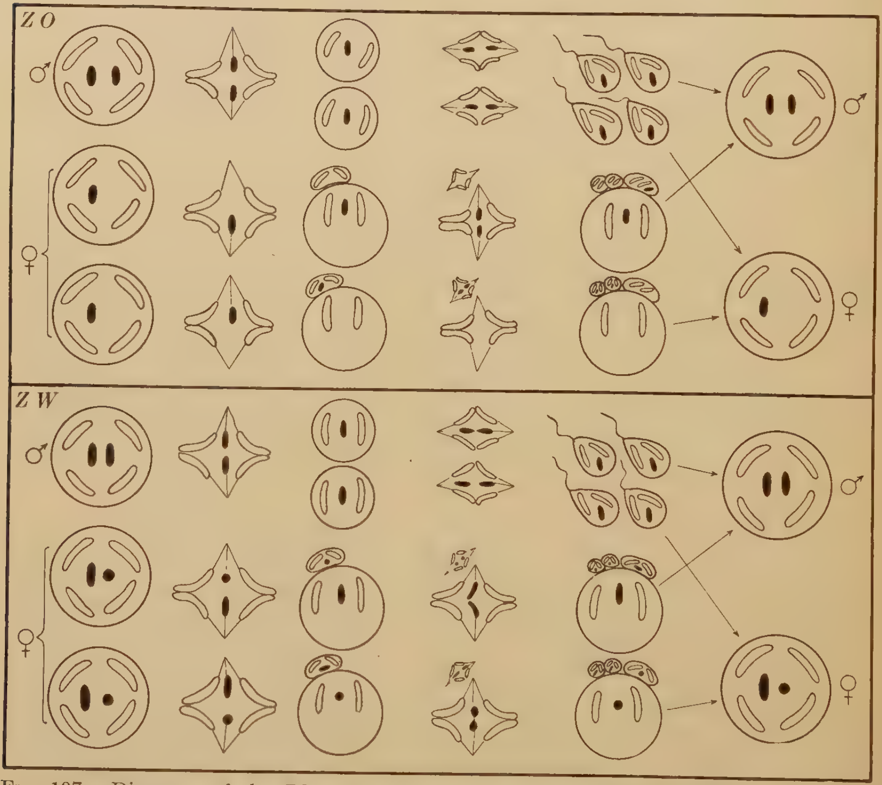

Fig. 197.—Diagrams of the *ZO* and *ZW* types of sex-chromosome behavior in animals. Division *I* is arbitrarily represented as disjunctional in all cases.

In *Abraxas grossulariata* Doncaster (1914) found that, whereas 56 chromosomes are usually present in the somatic nuclei of both sexes, the females of some strains have only 55 and produce two classes of eggs with 27 and 28 respectively. Agar (1920) thinks it not an unreasonable hypothesis that in the 56-chromosome forms the *Z* is paired with an inert *W*, and that the latter has been lost in the 55-chromosome strains.

In the case of the common fowl, cytologists are not yet in agreement as to whether the sex-chromosome differentiation is of the *ZW* or the *ZO* type.[1] The work of Stevens and Hance has apparently demonstrated the presence of a large unpaired *Z* in the nuclei of the female, but Shiwago reports the presence of a small *W*-chromosome also (Fig. 198). The number of autosomes is rather high (at least 15 pairs), and some of them are very small; this would tend to make the identification of a small *w* very difficult. The suggestion of Agar regarding *Abraxas* may be borne in mind in this connection. The situation in the male fowl is uncertain. According to Guyer (1909, 1916), a single large element passes to one pole in *I* and later to one-half of the spermatozoa, those without it degenerating. Morgan suggests that the large element is a pair of *Z*s, which disjoin in *II*, so that all functional sperms have *Z*. This point remains to be cleared up.

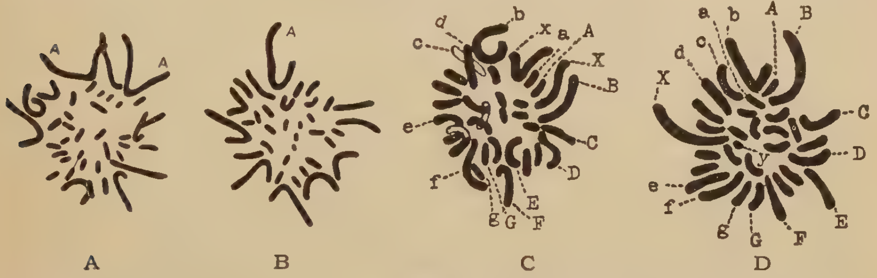

FIG. 198.—Chromosomes in the domestic chicken. Figures *A* and *B* from Hance (1924): two *Z*-chromosomes (marked A) in the male (left) and one in the female (right). Figures *C* and *D* from Shiwago (1924): in the male (left) is shown a *ZZ* pair (marked Xx), and in the female (right) a *ZW* pair (marked Xy).

*Other Evidence Relating Sex to Chromosomes.*—Brief mention may be made of additional data which point to internal factors, probably the chromosomes, as important agencies in the determination of sex. In Chapter XVI were cited several cases in which the sex of parthenogenetic animals is correlated with chromosome number. In *Hydatina senta*, for example, haploid eggs develop into males and diploid eggs into females. In the nine-banded armadillo one zygote commonly gives rise to four individuals, which are invariably all male or all female. Similar examples of polyembryony are known in insects. Human twins, if "identical" (produced by the same zygote), are invariably of the same sex; if "fraternal" (produced by different zygotes) they may or may not be of the same sex. Twins produced by dichotomy in *Arisæma* also tend to show the same sex manifestation, although this may be more readily altered than in animals (Schaffner, 1922*b*).

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[1] Stevens (see Boring, 1923), Hance (1924), Shiwago (1924).

Gynandromorphs afford further evidence of the rôle of chromosomes in sex-determination. Such individuals, with male characters in certain parts of the body and female characters in other parts, are known in several groups of animals which are normally unisexual, but most of them occur among insects. Even the gonads may be involved in such cases. In *Drosophila*, in which the hereditary rôles of the various chromosomes have been minutely studied by Morgan and his associates, such a bilateral gynandromorph as that shown in Fig. 199 seems clearly, on the basis of genetic evidence, to result from the elimination of one *X*-chromosome during an early embryonal mitosis in a female. One part of the body thus develops with *X* and the other part with *XX*, the autosomes in both parts being the same. Morgan thinks it probable that certain silkworm gynandromorphs described by Toyama may result from the fertilization of eggs with two nuclei by two spermatozoa, one with *X* and the other with *Y*. Three explanations have been offered for gynandromorphism in bees: the entrance of a spermatozoön into an already segmenting egg (Boveri); the entrance and independent development of a second spermatozoön in an already fertilized egg (Morgan); chromosome elimination as in *Drosophila* (Morgan).

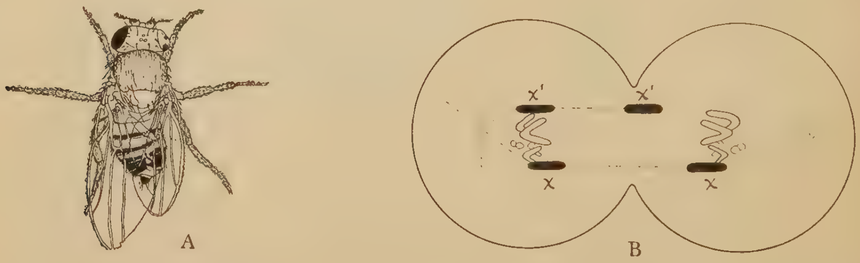

Fig. 199.—*A*, a *Drosophila* gynandromorph, female on the left side and male on the right. *B*, explanation suggested for this condition by Morgan: in an early cleavage one *X*-chromosome fails to be included in either daughter nucleus, so that the nuclei in part of the fly have *XX*, while those in the other part have *X*. (*After Morgan, Sturtevant, Muller, and Bridges.*)

**Summary.**—In the foregoing review it has been shown that there are many animals in which the individuals of the two sexes differ visibly in their chromosome complements. In some species there are two kinds of spermatozoa which differ in one or more of their chromosomes, whereas in other species this differentiation occurs in the eggs rather than the spermatozoa. In both cases the sex of the individual is definitely correlated with the type of gametic union which initiates development. This clearly indicates the dependence of sexual differentiation on an internal mechanism: *the chromosomes have a definite causal relationship with sex.* The closeness of this relationship, and the degree of fixity of the sexual states so established, are known to vary considerably in different organisms. The chromosomes are plainly important agencies in sex-determination, but they are by no means the sole determiners. This question will be discussed at some length later in the chapter.

**Metabolism and Sex.**—Although the sex of animals is by no means so amenable to environmental control as the uncritical interpretation of evidence has led many to believe, experimental biologists have nevertheless shown that the sexual states which are ordinarily related to the differential action of internal factors may be decidedly altered or even reversed in certain instances by appropriate changes in external factors acting through the metabolic processes. This has led to the view that the difference between the sexes is primarily one of metabolism—a difference not necessarily in the kind of metabolism as Geddes and Thomson suggested, but more probably in its rate or level. A few outstanding examples of metabolic sex control and reversal will now be cited.

In pigeons, two eggs are produced at each laying, the first under ordinary conditions developing into a male and the second into a female. Many years ago a study of the effect of nutrition on the sexual potencies of these eggs was undertaken by Whitman, whose researches have been continued by Riddle (1912, etc.) with very significant results. By an analysis of a large number of eggs it has been shown that the yolk of the first egg differs from that of the second in having a smaller size, a smaller amount of storage material (fats and phosphorus-bearing compounds), a higher water content, and a higher rate of metabolism, as indicated by oxidizing capacity. Whatever other differences may be present, *the sexes are characterized in the egg stage by different levels of metabolism, the male having the higher rate and the female the lower;* and studies on the metabolism of the blood indicates the persistence of this difference into the adult stage.

The seasonal change in the amount of storage, and consequently in the level of metabolism, is definitely correlated with the percentage of a given sex and the degree of its manifestation. As the season advances both eggs of the pair store more energy-containing materials, and the birds developing from the second (female-producing) egg, while often quite "masculine" in their secondary sex characters early in the season, become increasingly "feminine" toward the end of the season. Moreover, the total percentage of females meanwhile increases. By influencing storage, water content, and the general metabolic condition of these eggs, Riddle has been able to induce experimentally an actual reversal of their natural sex tendencies. Hence he concludes that sex is a quantitative, modifiable and "fluid" character: the two sexes do not represent two qualitatively distinct, mutually exclusive properties, but are rather two conditions of one general property—two levels in a continuous series of intergrading metabolic states. Genetic evidence indicates that the two levels are normally correlated with the *ZW* or *ZO* type of chromosome mechanism as in other birds, but Riddle has shown that they may be made to pass one into the other, with corresponding alterations in the manifestation of sexual characters. Complete functional sex-reversal as a result of ovarian tumors has been reported for the domestic fowl by Crew (1923), and Domm (1924) finds it occurring after ovariotomy.

In *Bonellia,* a gephyrean worm, the small and degenerate male lives parasitically upon the long proboscis and in the nephridium of the much larger female. If young individuals are kept in an aquarium by themselves they develop into females, but if they are placed with mature females they settle upon the probosces of the latter and develop into males. By allowing them to remain on the probosces for varying lengths of time many intergrades between the typical male and female conditions may be obtained. It is plain that the proboscis exercises an influence over the sex of the young animal, but whether this is through a secretion or some other agency is not known (Baltzer, 1914).

A somewhat similar case is that of *Crepidula plana,* described by Gould (1917). This mollusk is hermaphroditic but completely protandric, *i.e.,* the male and female phases are entirely separate in time, the former developing first. The development of the male phase is dependent upon the presence of a larger individual (not necessarily a female) of the same species. If a male is removed from the neighborhood of a larger individual the male organs degenerate, and after a period of sexual inactivity the animal becomes a female. The nature of the stimulus exerted by the larger individual has not been ascertained. In the phyllopod crustacean, *Simocephalus vetulus,* Banta (1916) finds that under certain experimental conditions "the same individual, even the same sex gland, may develop eggs and sperms at the same time or sperms at one time and eggs at another time." He also reports sex-intergrades in *Daphnia longispina* (1918).

The influence of hormones on sexual characters is strikingly shown in cattle twins, studied by F. R. Lillie (1917) and Lillie and Bascom (1922). Twins in cattle develop from separate eggs, and during the embryonic stages their blood systems are continuous. If both embryos happen to be of the same sex, development is normal, but if they are of different sexes certain hormones produced at an early stage in the interstitial cells of the testes of the male pass by way of the blood not only to other parts of the male embryo, causing the accentuation of masculine characters, but also to the female co-twin. As a result, the gonads of the female remain in a juvenile condition, and she develops into a sterile "freemartin" with certain masculine characters. As Lillie points out, sex in cattle is normally determined by genetic factors, but the natural sex-differentiation in the female may be arrested and to a certain extent reversed by sex hormones from the male.

The conclusion of Lillie is supported by the work of Minoura (1921) on chick embryos. If pieces of testes and ovaries are grafted on to the chorio-allantoic membranes of chick embryos, the reproductive systems undergo a number of modifications; whereas grafts of liver, thyroid, and other non-sexual tissues produce no such effects. It is accordingly inferred that the sex glands produce hormones with specific physiological functions, among which is an influence on the primary sexual characters. Okkelberg (1921) finds that young brook lampreys show various intergrades between maleness and femaleness and contain germ cells of both sexes, and that the sex of mature animals depends on the relative number of the two kinds of cells present. Secondary sexual characters are accordingly attributed to the action of sex hormones. This interpretation is also favored by Courrier (1921) for another fish.

The literature on sex-determination in amphibia has come to be one of considerable proportions.[1] There are many specific points which remain to be determined, but in general it appears that in frogs and other amphibians sex is normally dependent on inherited constitutional factors, but may be profoundly affected in its differentiation by hormones. Which sex is normally digametic has been a debated question. Results of certain breeding experiments involving sex-intergrades led some to the view that the male is digametic ($XY$ or $XO$) (Crew, Witschi), while a cytological examination of parthenogenetically developed males convinced Goldschmidt (1920*b*) that the female is digametic ($ZW$ or $ZO$). More recently Witschi (1924) has described what he interprets as an $XY$ pair splitting equationally in *I* and disjoining in *II*. It has long been known that overripeness of the eggs (high water content) and abnormally high temperatures lead to an excess of males in frogs and toads, and that the opposite conditions favor the development of females.[2] The masculine tendency of overripe eggs is attributed by Riddle to their male level of metabolism, as indicated by water content. Hertwig suggested that the abnormal conditions might cause the one $Z$-chromosome of the female to remain in the egg in more than the normal 50 per cent of cases. Whether or not such abnormal chromosome behavior actually occurs in amphibians is not known, but Seiler (1920) has shown that just such aberrations may be induced in a moth, *Talæporia tubulosa.* Heat and overripeness here result in a tendency on the part of the $Z$-chromosome to remain in the egg pronucleus more often than it is extruded into a polar body, whereas low temperature causes its more frequent extrusion. In the first case the eggs have one $Z$ and develop into males, and in the second they have no $Z$

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[1] R. Hertwig (1906, 1912), Kuschakewitsch (1910), King (1907–1912), Champy (1921, 1922), Goldschmidt (1920*b*), Crew (1921), Witschi (1923, 1924), Aron (1921), G. Hertwig (1920), Parmenter (1920), W. W. Swingle (1921).

[2] Delayed fertilization has been shown to affect the sex ratio in trout also (Mrsic, 1923; J. S. Huxley, 1923). Staleness of the sperm is found not to affect the sex ratio in pigeons (Riddle and Behre, 1921).

and develop into females. Mavor (1921–1923) has shown that $X$-rays may cause irregularities in the distribution of the sex-chromosomes in *Drosophila.*

Such facts naturally suggest that reversal of sex through environmental changes is accomplished through chromosomal aberrations, and that an organism does not actually develop the characters of one sex while it has the chromosome complement characteristic of the other sex. In some cases genetic data support this interpretation, but in others there is no evidence that the chromosome mechanism is altered in this fashion. In several instances intersexes are known to have normal chromosome complements, showing that at least some of the characters of one sex may develop in the presence of the complement normal to the other (Sturtevant, 1920; Goldschmidt, 1922). The remarkable series of intersexes in the gypsy moth, *Lymantria* (*Porthetria*) *dispar*, are explained by Goldschmidt (1916–1923) on the basis of genetic factors; but since the moths in question are hybrids, abnormal chromosome behavior is strongly suspected. The researches of Bridges on triploid *Drosophilæ*, which have done much to clear up the relation of chromosomes to intersexuality and normal sex inheritance, will be considered in the general discussion soon to follow.

In investigating the causes of sex-determination considerable care must often be exercised in order not to confuse actual determination of sex in the individual with certain other phenomena which may at first sight resemble it. Thus in many of the cases in which changed environmental factors have been shown to have an influence on the sex ratio it is clear that the results are not due to an actual reversal or determination of the sex in any individual, but rather to the fact that the new conditions imposed have caused a greater mortality among the eggs or embryos of one sex, so that those of the other sex preponderate. Although the ratio of the sexes may here be subject to an experimental control, the sex of no given individual is actually determined or altered.

Indirect control of another type is seen in organisms whose sex is dependent upon the form of reproduction (zygogenetic or parthenogenetic). Environmental conditions may in such cases influence the form of reproduction, and therefore the sex of the animal resulting; but the sex of no individual, once started, is altered. For example, the rotifer, *Hydatina senta*, if scantily fed on *Polytoma*, continues to produce generations of parthenogenetic females, but when copiously fed on *Dunaliella*, females appear which lay male-producing eggs, and sexual reproduction then occurs (Whitney, 1914, 1916). According to Shull and Ladoff (1916), the percentage of males is here correlated with the supply of oxygen which counteracts certain agencies (accumulated substances in the water) tending to decrease male production. Whitney (1919), however, contends that oxygen is not a factor affecting sex in *Hydatina*. As Morgan points out, the change of diet in *Hydatina,* instead of altering sex directly, induces the formation of a new type of female which may either function sexually or produce eggs which develop parthenogenetically into males.

Another case in point is that of *Dinophilus,* in which abnormal temperature conditions prevent the laying of the eggs from which one sex develops, without interfering with those giving rise to the other sex (Malsen, 1906). "If nutritive and other environmental influences are operative, it is, in the main, by affecting the production and survival of sexually predestined germ-cells" (Thomson, 1913). Such phenomena are to be kept distinct from sex-determination in the strict sense, *i.e.*, the control of the sex differentiated in any given individual, or a reversal of the sex after its development is already under way.

## THE FACTORIAL INTERPRETATION OF SEX-DETERMINATION[1]

**Mendelian and Metabolic Theories of Sex.**—As pointed out at the beginning of the chapter, there are in the field two rival theories of sex and its determination, which for convenience may be called the Mendelian and metabolic theories. According to the Mendelian theory, proposed shortly after the rediscovery of Mendelism, sex, like other characters of the organism, is regulated by an internal factorial mechanism. This view was considerably strengthened when it was found that in many animals (and later in certain plants) males and females differ visibly in their chromosome complements. It was natural to conclude that the chromosomes which are unlike in individuals of the two sexes, either of themselves or by virtue of "sex genes" contained within them, "determine sex" in the same way that other genes "determine" other characters.

The metabolic theory of sex was largely the outgrowth of many observations on the marked effect produced by alterations in environmental conditions, including nutrition and pathological states, upon the expression of sexual characters in a variety of organisms, both unisexual and bisexual. In some cases the effect was found to amount to complete sex-reversal (Riddle, Crew, Schaffner, Banta). The differentiations characterizing the two sexes, moreover, occurred in all sorts of combinations and "intergradations." Such facts were taken to mean that the two sexes are not fundamentally distinct characters due to the operation of an internal genic mechanism, but are rather intergrading physiological states (or consequents of such states), which either recur regularly at certain stages of development, or are set up at other stages by environmental conditions. This view is now held not only by opponents of Mendelism in general, but also by a number of investigators who admit the validity of the Mendelian theory for characters other than sexual ones.

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[1] This discussion with much that has preceded has been largely transcribed from the author's paper of the same title (1925).

The present problem, therefore, is to formulate a theory of sex which will embrace all of the above facts, and, by showing the relationship of these facts, to reconcile two conceptions, both of which contain elements of truth, but which appear mutually exclusive in the uncompromising form in which they are often stated. Adherents of each view are usually ready to admit that both "extrinsic" and "intrinsic" factors are somehow concerned in the process of sex-determination; there are few who have the hardihood to delimit the organism sharply from its environment and attribute any phenomenon to the action of either one alone. The real question is whether the "intrinsic" factors influencing sex are of the same general kind as those supposed to influence the development of other characters. Since the Mendelian interpretation is so freely admitted for characters other than sex, it will be well to ask first whether or not alterable states, such as the two sexes appear to be, and which manifest themselves in such a variety of combinations, can be accounted for by assuming the presence of "sex genes" in the chromosomes along with the genes affecting other characters.

**The Factorial Interpretation of Sex.**—Mendelian interpretations of sex until recently proposed have proved inadequate largely because they have been too simple. It has been found very difficult to formulate and reconcile with all the known facts any convincing hypothesis referring sex to the action of but one or two pairs of genes in a single pair of chromosomes.[1] Evidence recently brought to light seems to indicate clearly that sex, like other characters, is influenced by a larger number of genetic factors, and that these cannot be confined to one pair of chromosomes. Most noteworthy in this connection are the researches of Bridges (1921, 1922) on *Drosophila melanogaster* and of Emerson (1924) on *Zea Mays.*

Because of the conditions normally present in *Drosophila* it was long supposed that sex was a matter of the $X$-chromosomes alone, one of these causing maleness and two femaleness. As a result of his investigations on triploid flies Bridges has demonstrated that the two sexes are correlated not simply with the number of $X$-chromosomes present, but rather with the numerical ratio between these and the autosomes, as had for some time been suspected. Individuals in which the ratio is 1:2 (one $X$ to two autosome sets) are male; those with 2:2 or 3:3 are females (diploid and triploid). An intermediate ratio, 2:3, is correlated with the intersexual state, while flies with the extreme ratios 3:2 and 1:3 are "superfemales" and "supermales" respectively. (It is the opinion of Schrader and Sturtevant (1923) that the algebraic sum of the $X$-chromosomes and autosome sets, rather than their numerical ratio, is the effective relation in this case.)

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[1] See the papers of Goldschmidt (1919, 1920, 1921), G. Hertwig (1921), G. and P. Hertwig (1922), and Valleau (1923).

Bridges interprets his results, especially when viewed in the light of effects produced by parallel irregularities in autosome behavior, to mean that both sexes are due to the simultaneous action of two opposed sets of genes, whose influences on the organism are toward maleness and femaleness respectively. These genes, which may affect other characters also, must lie in most if not all of the chromosomes of the complement; the *X*-chromosome is peculiar merely in having a preponderance of the genes tending to produce female characters. The balance is such that, if the number of *X*-chromosomes equals the number of autosome sets, the female-producing genes in the complement as a whole outweigh in effect the genes tending toward maleness, and the individual is consequently female; whereas, if there are only half as many *X*-chromosomes as autosome sets, the female-producing genes present are insufficient to accomplish this result, and the individual is male. Intermediate and extreme ratios would be expected to produce the results actually observed. Since this is precisely what is found in the case of characters other than sex, Bridges concludes that "the conception of the nature and action of genes as gained from the study of non-sexual characters is valid in interpreting sex phenomena."

The foregoing explanation enables one to understand why the rarity of polyploidy among animals as compared with plants has been attributed to the activity of sex-chromosomes (p. 390). As Muller (1925) points out, the addition of an extra set of chromosomes would seriously disturb the normal balance between *X*-chromosomes and autosomes in the heterozygous sex. In *Drosophila*, for example, the ratio would be normal in the female (3:3 = 2:2), but in place of normal males (1:2) there would be supermales (1:3) and intersexes (2:3). Conversely, in organisms characterized by the *ZW* type of sex inheritance the males would be normal and the females aberrant. Such an abnormal condition in one sex might well be expected to offer a serious obstacle to the establishment of a triploid race, or of any other races with odd numbers of chromosome sets, in organisms with sex-chromosomes. The origin of tetraploid directly from diploid races, on the other hand, might be expected to occur more frequently, since a duplication of all the chromosomes would not affect numerical ratios. Noteworthy in this connection is the genus *Populus*, in which there are diploid, tetraploid, and hexaploid species, as well as sex-chromosomes (Blackburn and Harrison, 1924*a*; Meurman, 1925).

With regard to the case of *Zea Mays*, Emerson (1924) writes as follows:

> The genetic situation in maize, though on the whole much less well known than that in *Drosophila*, may perhaps afford some help toward a solution of sex problems. Normal maize plants are monœcious, with maleness expressed in the terminal and femaleness in the lateral inflorescences. There are, however, mutant types of maize which, under ordinary conditions, are wholly female, the

terminal as well as the lateral inflorescence bearing pistillate flowers only. Four distinct recessive genes are known, the influence of any one of which results in femaleness. Moreover, two of these have been definitely placed with respect to genes for such characters as color of seeds, color and form of leaves, and the like, and their *loci* are in non-homologous chromosomes. Although no entirely male strains of maize are known, there are three types which ordinarily produce only a few pistillate flowers and some individuals of which have no such flowers. And each of these again is due to one or more recessive factors, each one being transmitted independently of the others. Moreover, there are two types in which the normal monœcious condition has been modified to an andromonœcious one; and each of these two types also is due to the influence of one or other of two recessive genes. In all, then, there are at least nine pairs of genetic factors which influence the expression of sex in maize.

It is not yet known whether all these nine pairs of genetic factors are to be assigned to nine of the ten pairs of chromosomes, but certainly several of them are inherited independently. Although no diœcious strain of maize is known to exist and the sex situation in this plant may not be closely similar in some other respects to that in *Drosophila*, it none the less adds to the plausibility of the present interpretation of sex, namely, that sex is probably an expression of the interaction of several, perhaps many, factors located in different chromosomes. In any event sex inheritance is not the simple affair that it has been supposed to be. In this respect, sex inheritance corresponds closely to the hereditary behavior of other characters.

If, therefore, as the foregoing data indicate, sex inheritance is to be referred to chromosomal genes, the differentiation of the sexual characters (the "expression of the sexes") in the ontogeny will depend on the proportion of female-producing and male-producing genes present, and on the manner in which this complex of genes operates under the conditions prevailing during development, such operation varying with the conditions at different times and regions in the organism. The sexual state of an organism is consequently determined by a combination of two processes: (1) the establishment of a complement of genes affecting sex, through segregation at meiosis, or aggregation at syngamy, or both; and (2) the action of these genes in coöperation with other elements of the interacting system in the course of ontogenesis.

Since the result produced by the interacting system is due in the first place to the constitution of that system, which is in large measure inherited, and in the second place to the manner of its action, which can be influenced within certain limits through external agencies, the determination of sex, like that of other heritable characters, involves the interaction of two sets of factors: (1) *genetic factors* (inherited germinal constitution; intrinsic factors; genes); and (2) *non-genetic factors* (extrinsic factors; environmental agencies, external and internal).

**The Conception of Differential Factors.**—In any heterogeneous system, constituent elements or factors of various kinds contribute in different ways and in different degrees to the resultant action of the system as a whole. If some process is found to vary with the alteration of one factor (or group of factors) while the other factors remain relatively constant or show in their variation no differential effect upon the process, that one factor (or group) may be said to be the *differential factor* for that process under the given conditions. Under other conditions, which may cause a change in the operation of the system as a whole, the process in question may be found to vary with the alteration of some other factor. Thus it is now one factor, and now another, which is differential (or limiting, or controlling) for the process. In many instances, moreover, factors of different kinds may act differentially at the same time, the effect upon the course of the process being the resultant of their influences. But in no case can the factors which are not varying or acting differentially be for that reason denied a share in the determination of that process: the process depends upon the action of the whole system, all or nearly all of whose component elements are necessary to this action and hence to the process. Factors may therefore be conditioning without being differential.

The bearing of this conception on the problem of the development of sex and other inherited characters should be obvious. In a previous chapter (p. 376) emphasis was laid upon the fact that in an organism the genetic and non-genetic factors together constitute a system in which different elements may act in a differential or limiting capacity under different circumstances and in connection with different characters. With regard to sex, all of the inherited factors (genes) and all environmental agencies affecting their action together constitute the system producing the results observed. As Riddle (1917) states, organisms have had the problem of producing germs of two metabolic levels, and in some cases this has led to the establishment in the two sexes of two amounts of karyotin or even of different types of chromosome complements. The sex-chromosomes, or units contained within them, act with others in the maintenance of two diverse levels of metabolism in the gametes and in the offspring, and with these levels are correlated the two conditions commonly distinguished as male and female. Where genes tending respectively toward maleness and femaleness are more or less equally balanced in influence, one may expect the modification of the sexual characters to be more readily accomplished through alterations in the non-genetic factors of the system than where the genes of one tendency greatly predominate, or especially where the differentiation of the sexes has come to involve visible differences in chromosome complements. One should expect various degrees of fixity of sexual characters in different organisms, and such are actually found. The genic difference being only one factor in a complex system producing the two sexual states, and no single element in this system being the sole determiner of sex, it is not strange that the effect of this one factor should at times be annulled by sufficiently altering the other factors, thus modifying the action of the factorial system as a whole.

In organisms with definitely differentiated sex-chromosomes the sex of the individual under all ordinary circumstances is dependent on the kind of sperm (or, in some cases, the kind of egg) functioning in syngamy, and ordinarily does not change thereafter. So far the chromosome theory is valid; but it does not follow from this that sex, which is characterized by a certain physiological state, and which is correlated with a certain type of chromosome complement and a variety of secondary sexual characters, is so firmly fixed that it cannot be altered by any extraordinary means. The metabolic state, even though its regulation may be accomplished in part through a visible mechanism, is the resultant of a complex series of reactions which may be interfered with at many points. It is admitted that other heritable characters definitely associated with constant genes are greatly modified in the manner and degree of their expression by environmental influences, and the evidence at hand indicates that no exception to this rule is to be made in the case of sex. The effects of heredity and environment are not so much opposed as complementary.

It is scarcely necessary to point out that neither genes nor environmental factors are to be thought of as producing their effects upon sexual or other characters directly. Their influence is exerted rather through the intermediary of a long and complicated series of intracellular and intercellular reactions. Upon some of these reactions, notably those involving endocrine secretions in animals, certain researches are throwing considerable light; some investigators think it probable that hormones play a rôle in determining sex in plants also (Riede, 1922). The nature of most of the intermediate changes, however, remains largely a subject of conjecture.[1] The important point is that the physiological states which regularly recur at the time of the differentiation of the sexual characters, and which manifest themselves largely in cytoplasmic and intercellular changes, are not to be regarded as independent causes of that differentiation, but rather as members of an orderly succession of states which owes its existence to initial germinal structure as well as to environmental factors. The fact that such emphasis is placed upon these two fundamental groups of factors in this discussion should not be taken to mean that one is to minimize the importance of those processes which stand between the factors and the ultimate results of their action.

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[1] Of great interest is the recent discovery by Manoilov (1922-1923) of a reaction which demonstrates a chemical difference in the blood of male and female animals. The reaction also shows a difference in the chlorophyll of staminate and pistillate angiosperms (Manoilov; Grünberg, 1922–1923). The findings of these authors have been confirmed by Satina and Demerec (1925). Minenkov (1924) has described a second method showing the difference in heterophytic angiosperms. Dr. F. B. Wann finds that Manoilov's reaction demonstrates a chemical difference between male and female gametophytes of the heterothallic liverwort, *Marchantia polymorpha.*

Since the effects of environmental factors are produced through metabolic processes, it is obviously impossible to distinguish sharply between "external" and "internal" factors at the point where they are actually functioning; both operate "internally." The environment must therefore be thought of as permeating, rather than merely surrounding, the organism. The two maintain throughout the life cycle a relation which precludes any complete separation, as has already been pointed out. Each part of the organism, moreover, is an element in the "environment" of other parts, and may affect them by various means. Genetic and environmental factors respectively may influence different reactions which are integral parts of one more general process, or members of the two sets of factors may affect directly the course of the same individual reaction. It is this intimate association of the factors that requires one to conceive of them as constituting *a single interacting system*, no result of whose operation is safely to be attributed to a single component element, even though that element may be the sole differential factor.

## APPLICATION OF THE FACTORIAL THEORY TO LIFE CYCLES

According to the non-Mendelian interpretation of sex, as stated by Schaffner and others (see Fig. 188, first diagram), sex is "determined" at a single point in each cycle: late in the development of the gametophyte in forms like the synoicous mosses (1), earlier in paroicous species (2), still earlier in autoicous species (3, 4), and at the point of meiosis (5) in dioicous species. It then continues to "move backward" through the sporophyte phase, giving the wide range of conditions seen in seed plants (6–11), until finally the point of syngamy (12) is reached; the sporophyte then becomes unisexual also. At whatever stage the determining process occurs—whether at meiosis, syngamy, or any other point—it is the same in nature, consisting essentially of physiological reactions controllable in various degrees in different species. Furthermore, it is in all cases independent of any system of Mendelian factors or genes, because (*a*) the sexes are "determined" or "separated" at any point, whereas the Mendelian factors segregate at only one point; and (*b*) the sex manifestations are too variable in kind and modifiable by environmental conditions to be the result of the action of an internal mechanism.

We shall now outline the Mendelian interpretation of several types of life cycles, bearing in mind the cases reviewed in the historical résumé.

**Homothallic Bryophyte** (Fig. 188, third diagram).—In a homothallic bryophyte (or pteridophyte) all of the gametophytes are alike in producing both male and female gametes. The gametes are differentiated at times and regions which differ widely in different species, giving the synoicous, paroicous, and autoicous conditions. The development of each sex is the result of the influence of certain environmental (external or internal) factors upon the germinal constitution of the tissue in a given region of the plant at a given stage. That there is no segregation of germinal units or genes at this stage (*a*) is evidenced by the experiments of Correns and of von Wettstein, as well as by frequently observed bisexual organs. That any segregation of sex genes which may occur at meiosis (*m*) is not differential is evidenced by the similarity and bisexuality of all the gametophytes; homothallic species are thus homosporic. Since the complement of sex genes is the same in all parts of each gametophyte, and virtually so in all gametophytes, this is a case in which the differential factors in the system are the non-genetic ones. Hence these are the "differential cause" of the sex expression, but they are by no means solely responsible: they are not its whole cause. The very fact that the sex expression in such plants is often so difficult to alter indicates the rôle of the germinal constitution, which the Mendelist calls the "gene complex" and the non-Mendelist the "predisposition." The genes are conditioning factors, although they may not in this case be differential factors. Whatever occurs is the resultant of the interaction of both sets of factors, *i.e.*, it is a product of the entire system. When it is said that in such cases "environmental factors determine sex" one means simply that these factors are the differential ones in a system including also other conditioning factors, all of which are in some measure responsible for the phenomena observed. The statement that "sex is determined at the time the sex organs appear" means only that at this point (*a*) in the cycle certain tissues realize some of their inherent capacities. The misleading expression "separation of the sexes" indicates neither a differential division of the germinal mechanism nor an actual separation of anything previously together, so far as known, but merely the development of two kinds of sexual characters in different regions by tissues with similar germinal mechanisms. There is probably no fundamental difference between this and the ontogenetic differentiation of other characters.

**Heterothallic Bryophyte** (Fig. 188, fourth diagram).—In a heterothallic bryophyte there are produced two distinct kinds of gametophytes, bearing male and female sex organs respectively. These gametophytes develop from two kinds of spores which are produced in equal numbers. It has been shown in certain cases that two spores of a single quartet have the female predisposition, and two the male; such forms are heterosporic but homosporangic. In *Sphærocarpos* this is correlated with a visible chromosome difference: the first meiotic division is differential for $X$ and $Y$ chromosomes, the two spores with $X$ developing into female gametophytes, and the two with $Y$ into males.

The fact that the two kinds of spores develop into gametophytes with unlike sexes under the same general conditions shows that one meiotic division is differential for sex tendencies, or, as the Mendelist prefers to say, sex genes. Moreover, the fact that this occurs under a wide range of environmental conditions—*i.e.*, the fact that sex is often so "fixed" here—shows that in such heterothallic species the differential factors are under all ordinary circumstances intrinsic, and involve differences in the germinal material that in some cases are visible. The further fact that the sex expression in such cases can sometimes be changed by altering the environmental factors sufficiently, *i.e.*, the fact that an individual predisposed toward one sex can be made to develop the other sex or both sexes, shows (1) that the genes with the two tendencies are in such cases not completely segregated in meiosis, every haploid nucleus carrying male and female sex factors in some proportion; and (2) that the action of the whole interacting system can be so altered that the environmental factors become the differential ones in place of, or together with, the genetic factors.

The experiments of the Marchals are usually said to demonstrate that in the case of the heterothallic mosses "both sex tendencies are present" in the sporophyte and are "separated" at sporogenesis, so that "only one sex tendency is present" in any gametophyte. To the Mendelist this means that the genes influencing the development of male and female characters are rather evenly balanced in the diploid chromosome complement, whereas in the haploid complement of the gametophyte those with one tendency far outweigh in effect those of the other. At the time of meiosis the segregation of genes must consequently be highly differential in such strongly heterothallic species, instead of equational or nearly so as in homothallic forms.

Thus the expression, "sex is determined at meiosis," means that it is at this point that the particular assortment of inherent capacities (to develop a certain sex, among other things) of the gametophytes is determined, half of these being male and half of them female under similar environmental conditions ordinarily prevailing at some future time. The expression, "genetic factors determine sex," in this case signifies only that these factors are the differential ones under normal conditions for these plants. The non-genetic factors can no more be neglected here than can the genetic ones in cases where environmental factors are differential. The whole of the process of sex-determination includes the effects of both sets of factors in both categories of cases.

**Homophytic Seed Plant** (Fig. 188, fifth diagram).—In all seed plants there are two kinds of gametophytes, male and female, which differ greatly in morphological and physiological characters, and which have not been seen to alter their sexes under any circumstances. These two kinds of gametophytes arise regularly from two sorts of spores (megaspores and microspores); but these two sorts of spores are not the result of a differential division at the time of quartet formation, as they are in heterothallic bryophytes. They are formed rather in separate complete quartets, which in homophytic species are produced on the same sporophyte body, often very close together. Such plants are therefore homophytic, heterothallic, heterosporic, and heterosporangic.

The differentiation of the two sorts of quartets does not indicate a segregation of genetic factors (at *b*), since the microspores and megaspores are known by breeding to carry, on the whole, the same hereditary potentialities, however greatly the individual spores of one sort may differ among themselves as the result of the segregation of genes known to occur at meiosis, and in spite of the difference in the morphology of the gametophytes of the two sexes. Why, then, do the two sorts of spores differ in what they produce when their gene complements are essentially the same? The answer must be fundamentally the same as that to the question of the differentiation of the two kinds of sex organs on the same gametophyte in homothallic bryophytes. In the presence of the same complex of genes the plant produces megaspores and microspores as a result of the differential action of unlike sets of physiological or non-genetic factors acting through the cytoplasm in different regions. The two sorts of spores come to differ so greatly in their morphological and physiological characters that the resulting gametophytes differ in morphology and sex in spite of the general similarity in their gene complexes, the minor differences in the complexes of individual spores of one kind brought about at meiosis not having any visible effect upon the sexuality of the gametophytes. If there were a differential segregation of sex factors at meiosis (*m*) there would be more than one kind of sporophyte.

In the homophytic seed plant, as in the homothallic bryophyte, the differential factors in the sex-producing system are the non-genetic ones. In the case of the seed plant, however, these factors set up two physiological states at a stage in the ontogeny of the sporophyte, causing it to produce two sorts of spores; and these states either continue into the gametophytes or are regularly succeeded by other states which are correlated with, or actually represent, maleness and femaleness. The "separation of sexes" at the point *b* in the cycle means only the differentiation of two sorts of spores in different regions of the sporophyte.

This interpretation receives strong support in the situations found in certain heterosporangic pteridophytes, which have this type of life cycle. In *Selaginella* the sporangia are all essentially alike up to the sporocyte stage. If all of the sporocytes continue to develop, numerous microspores result; if all but one cease to develop, a single megaspore or megaspore quartet results. Hence, whether the cells in the sporangium give rise to megaspores or to microspores seems to depend upon the conditions surrounding them, particularly those conditions favoring a disintegration of some of the cells. This is further indicated by the results obtained in *Marsilia* by Shattuck (1910), who was able to produce a number of intergrades between megaspores and microspores by subjecting the plants to the effects of a cold spray. Under ordinary circumstances the conditions favoring the development of two types of spores occur in rather definite relative locations within the sorus (*Marsilia*) or strobilus (*Selaginella*).

**Heterophytic Seed Plant** (Fig. 188, sixth diagram).—In the life cycle of a heterophytic seed plant there are not only two kinds of gametophytes, male and female, but also two kinds of sporophytes, producing microspores and megaspores respectively. Such plants are therefore both heterothallic and heterophytic.

The reason for the occurrence of two kinds of gametophytes must be in large measure the same as that for the homophytic cases just dealt with; female gametophytes develop from megaspores and male gametophytes from microspores, in spite of the general similarity of their genotypes. There are reasons, however, for assigning more differential value to the genes here than in the case of homophytic seed plants, as will be seen in considering the factors controlling spore production in the sporophytes.

The two kinds of sporophytes arise from two kinds of zygotes, which differ because of a dissimilarity in the male gametes concerned in their formation. In some species these two kinds of gametes are known to be the result of a differential division at the time of meiosis in the microsporocytes. Such species are therefore dimorphic as regards their microspores, male gametophytes, and male gametes, and one may speak of them as disporic and digametic. In certain cases visible chromosomal differences are involved: some microspores, and hence some male gametes, carry an $X$-chromosome, and some carry a $Y$-chromosome. All of the eggs are alike in carrying one $X$-chromosome as the result of the disjunction of two $X$-chromosomes in the megasporocyte. In syngamy two sorts of combinations are possible: $XX$ and $XY$. Zygotes with these two combinations develop into sporophytes bearing megaspores and microspores respectively. Since these two classes of plants develop under the same general conditions, and are often very resistant to the influence of environmental factors, it is concluded that the germinal constitution, or gene system, is here the differential factor in the process determining the kind of spore a given sporophyte shall produce under ordinary conditions. In this sense the staminate and carpellate conditions in the sporophytes are "determined" by differences in the genetic complexes which are often correlated with visible dissimilarities in the chromosome complements. But the fact that environmental factors do in many cases influence the sex expression, even in forms with sex-chromosomes (*Humulus japonicus*), shows that these factors are conditioning factors which in some cases can be made differential.

**Animal** (Fig. 188, second diagram).—Except for the absence of spores and gametophytes, the life cycle of the animal closely resembles that of the heterophytic seed plant. Earlier in the chapter it was stated that many animals are distinctly digametic, producing two kinds of male or female gametes, often with visibly different chromosome complements. There can be no doubt that in such cases the differential factors concerned in sex-determination are the genetic ones. Under all ordinary conditions the sex of the individual depends on which kind of spermatozoön (or egg, in species with digametic females) functions in syngamy, so that it is commonly said that "sex is determined at fertilization." The degree of fixity is probably greater than in most plants, but experiments in sex modification and reversal indicate that here, too, the non-genetic factors are at all times in some measure concerned, and may in some cases be made to act differentially. Hence there appears to be no reason to suppose that the principles outlined in the foregoing pages are not as applicable to this and other types of animal life cycles as they are to the cycles of plants.

**Summary.**—In bisexual organisms the gene complexes in all individuals are nearly enough alike (with respect to genes affecting sex) that these will show the same sex manifestation under similar general environmental conditions; and the constitution of this gene complex is such as to result in the production of both sexes as responses to the different special conditions in tissues in different regions, or at different stages of development. Artificial modifiability here depends on the extent to which those particular special conditions, which are in this case the differential factors, can be controlled or altered.

In unisexual (diœcious) organisms the gene complexes of some individuals differ from those of others in such a way that some develop one sex, and others the other sex, under the same general environmental conditions, and in the presence of the range of special internal conditions normally prevailing. Under ordinary conditions, therefore, it is the genetic factors that are differential. In the heterothallic bryophytes the segregation of genes at meiosis results directly in spores and gametophyte individuals of the two sexes; in heterophytic seed plants it results in two sorts of microspores and hence male gametophytes, whose respective gametes cause a difference in the sex expression of the succeeding sporophytes; in animals it results directly in two kinds of gametes of one sex. Artificial modifiability here depends on the kind and degree of difference between the male and female gene complexes, and on the extent to which their differential effect can be overcome by altering controllable extrinsic factors of the system, *i.e.*, the extent to which the latter factors can be made to assume or to share in the differential function.

## CONCLUSIONS

1. In view of the evidence so far afforded by organisms with life cycles of different types, one must regard as inadequate any theory that

sex-determination is due exclusively and in all cases to the same set of differential factors, whether these be genetic or environmental in nature.

Any general theory applicable to all cases must account for sex-determination as the result of the interaction of two sets of factors: genetic factors, represented by the inherited physico-chemical organization of the protoplasm, and non-genetic factors, represented by the environmental conditions with which this organization is inseparably associated. These two sets of factors, which are integral parts of *a single organic system* producing the phenomena in question, vary in the relative proportion of their respective differential or controlling effects upon sexual differentiations in different types of organisms, and in the same organism under appropriately dissimilar conditions.

2. The evidence further indicates that the genetic factors influencing sex can at present be profitably treated as genes of the same general nature as those held to function in the inheritance and determination of other characters; hence sex inheritance may be regarded as Mendelian in nature.

3. Disproof of Conclusion 2, or even disproof of the current theory of the mechanism of Mendelian heredity in general, would not invalidate Conclusion 1.

# CHAPTER XX

## LINKAGE

In Chapter XVII attention was directed to the remarkable parallelism which exists between the distribution of the Mendelian characters and that of the chromosomes through successive generations. Breeding experiments with both plants and animals have shown that new combinations of characters result from the union of nuclei in syngamy, when two parental sets of chromosomes are brought together, and that a segregation of characters occurs as a result of meiosis, when the chromosomes are sorted into two groups. Moreover, the distribution of a single allelomorphic pair of Mendelian characters parallels precisely that of a single homologous pair of chromosomes. These facts indicate clearly that chromosomes and characters are in some manner causally related. This conclusion is strongly supported by the cytological aspects of sex inheritance, maleness and femaleness in a large number of reported cases being definitely correlated with the activity of certain distinguishable chromosomes.

It has also been pointed out that the hypothesis upon which these phenomena are generally interpreted is that the characters are represented in the chromosomes by material factors, or genes, which in some way influence the development of characters in the individual. Since an organism has many more Mendelian character pairs than chromosome pairs, one pair of chromosomes must, as a rule, carry genes for more than one pair of characters. Furthermore, the different pairs of chromosomes are entirely independent of one another in distribution. It would therefore follow that if two allelomorphic character pairs have their principal genes located in different chromosome pairs, they will be quite independent of each other in their inheritance through a series of generations, being transmitted together in 50 per cent of the cases on the average; whereas, if their genes are located in the same pair of chromosomes, they will be inherited together. Such a persistent association of genes or characters belonging to different allelomorphic pairs through a series of generations is known as *linkage*.

The phenomenon of linkage, or "coupling," was discovered in 1906 by Bateson and Punnett in the sweet pea. They found flower color to be linked with the shape of the pollen grain: purple flowers nearly always had long grains, while red flowers had round grains. The possible relationship between linkage and the chromosome hypothesis was pointed out by Lock in the same year. Linkage relations have since been worked out in a considerable number of plants and animals, and are especially well known in *Drosophila* and *Zea.*[1]

**A Typical Case of Linkage.**—As a typical example may be taken the following case of linkage in *Drosophila* (Fig. 200). A male fly with white eyes and yellow body is mated to a female with red eyes and gray body. The flies of the $F_1$ generation all have red eyes and gray bodies, since red is dominant over its allelomorph white, and gray is dominant over its allelomorph yellow. If the females of this generation are "back-

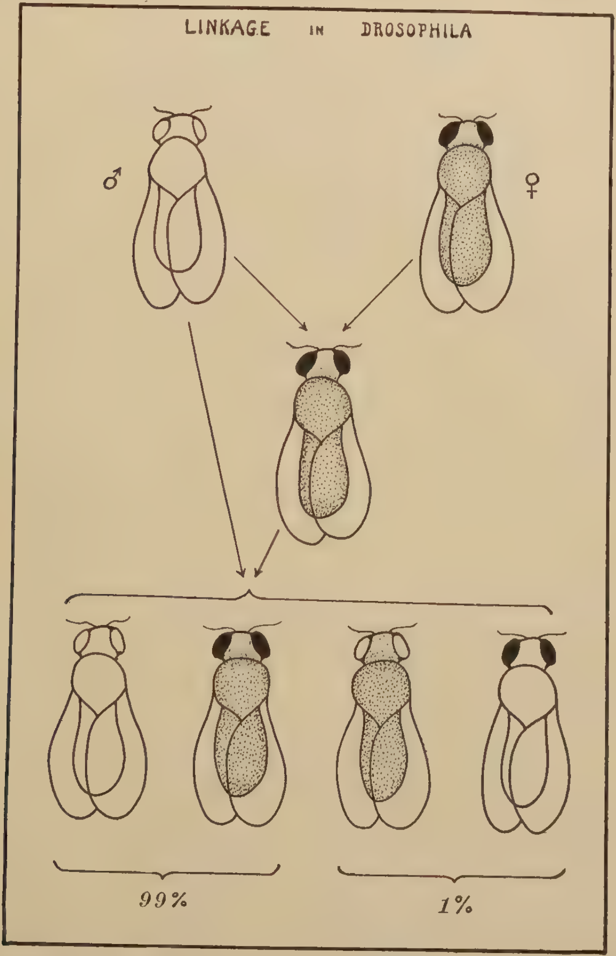

Fig. 200.—Linkage in *Drosophila*. Red eyes in black; gray bodies stippled; white eyes and yellow bodies unshaded.

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[1] For the literature on linkage in *Drosophila*, see Morgan *et al.* (1922), Bridges and Morgan (1923), Metz *et al.* (1923). For *Zea*, see the résumé by Lindstrom (1923.)

crossed" to males with both of the recessive characters,[1] white and yellow, flies of four types appear in the next generation, as shown in the diagram: white-yellow, white-gray, red-yellow, and red-gray. Since one parent in this last cross is a double recessive, these results show that the $F_1$ red-gray female must produce eggs of these four genotypic constitutions.

All four types, however, are not produced in equal numbers. Those flies with the same combinations as were shown by their grandparents, white-yellow and red-gray, together comprise 99 per cent of the total number; only 1 per cent show the other possible combinations, white-gray and red-yellow. It thus appears that if the two characters, red eyes and gray body, are contributed to the offspring by the same parent, they come out together in the second generation in nearly all cases; they are definitely linked, and this is explained on the hypothesis that their principal genes are located in the same chromosome. The same is obviously true of their respective allelomorphs, white eyes and yellow body; their genes are carried in the other chromosome of the homologous pair. Were the two allelomorphic pairs of genes carried in different pairs of chromosomes there would be no such linkage: the two characters, red and gray, and similarly the two characters, white and yellow, would then be exhibited together by 50 per cent of the flies, the chance frequency, rather than 99 per cent. How it is that the linkage is broken, in some cases giving 1 per cent with exceptional combinations, is a question to be discussed later in the chapter.

**Sex-linkage.**—A very interesting special case of linkage is seen in sex-linkage, which may be illustrated by the following example (Fig. 201) (Morgan, 1910). If a red-eyed wild male is mated to a white-eyed female (a member of a race descended from white-eyed mutants) the $F_1$ individuals are white-eyed males and red-eyed females—each eye color has been transferred from one sex to the other, a case of "criss-cross" inheritance. If these $F_1$ flies are bred together, the $F_2$ generation comprises four types: red-eyed males and females, and white-eyed males and females. If the distribution of the sex-chromosomes is followed through these generations, this striking fact is revealed: red eye color appears in every fly, male or female, which possesses the $X$-chromosome of the original red-eyed male; and white eyes appear in every male which receives one of the $X$-chromosomes of the original white-eyed female, and in every female receiving two of them. This means that the original male's $X$-chromosome carries a dominant factor for red eyes, while each of the $X$-chromosomes of the original white-eyed female carries a recessive factor for white eyes. In all the (diploid) flies it is seen that the presence of one $X$-chromosome is correlated with maleness, and that of two $X$-chromosomes with femaleness (compare Fig. 194); and that the two types of eye color under consideration follow the distribution of these chromosomes—they are *sex-linked characters*.[1] This general interpretation is directly applicable to the reciprocal cross (white-eyed male × red-eyed female), in which, however, the relative proportions of red-eyed and white-eyed flies in $F_1$ and $F_2$ are different. In $F_1$ all flies of both sexes have red eyes, while in $F_2$ all of the females and one-half of the males have red eyes, white eyes appearing only in one-half of the males. The failure of white eyes to appear in the females of $F_2$ marks this character as sex-linked.

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[1] This back-crossing to the pure recessive is the common method of testing the genetic constitutions of hybrids.

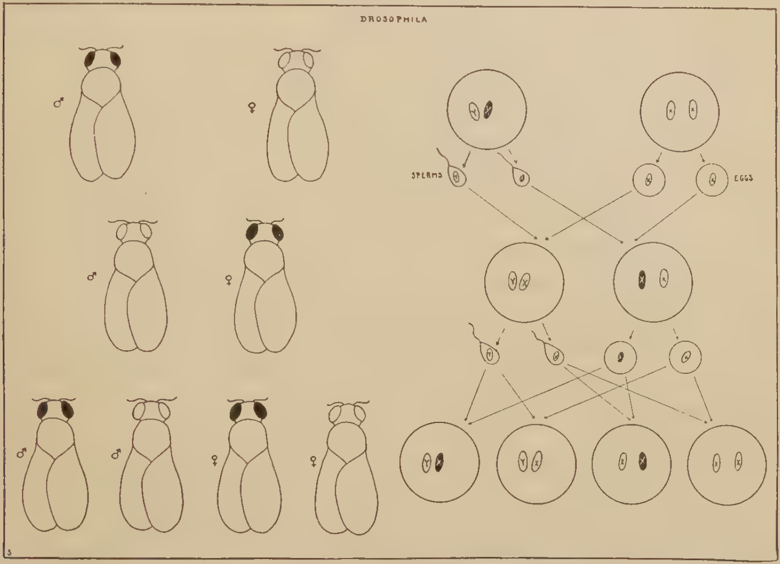

Fig. 201.—Sex-linkage in *Drosophila*. Three successive generations at left; red eyes shown in black. History of sex-chromosomes through these generations shown at right, the $X$-chromosome of the original male in black. (*Adapted from Morgan.*)

In such cases as the above it is evident that characters other than sex may be referred to certain chromosomes of the complement. It is possible not only to tell which chromosomes produce the principal effect on sex, but also to identify the ones mainly concerned in the production of red and white eye colors. A large number of such sex-linked characters have been identified in *Drosophila*, and several have been found in other organisms. Human colorblindness is such a character. The presence of this defect more commonly in men than in women, and its appearance in so few individuals in affected lines, are due to the fact that it is both a recessive and a sex-linked character, precisely like white eyes in *Drosophila*. It occurs in a woman only if both of her *X*-chromosomes bear factors for it, which means that one such factor must have been received from each parent; whereas one factor is sufficient to produce colorblindness in a man, because his *Y*-chromosome carries no factors which might dominate it. Furthermore, since the *X*-chromosome of the male is always derived from the mother, a man can inherit colorblindness from his mother but not from his father. He might appear to do so, however, if his father were colorblind and his mother apparently normal but carrying one affected *X*-chromosome; the defect in this case would actually be transmitted by the mother, though apparently by the father. In general, therefore, a colorblind woman transmits the defect to all of her sons and to half of her grandsons and granddaughters, whereas a colorblind man transmits it to none of his children and only to one-half of his grandsons. This interpretation has recently been confirmed by Schiötz (1920).

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[1] Sex-linked characters are not be confused with sex-limited characters. The latter are those found exclusively in individuals of one sex, and are usually called secondary sexual characters. In several cases it has been shown that their genes are located in the autosomes (see Morgan, 1914, 1919*c*, 1920). It is suggested by Winge (1922*a*) that inheritance of secondary sexual characters through autosomes be referred to as "sex-limited" inheritance, that of characters through the sex-chromosome common to both sexes ($X$ or $Z$) as "sex-linked" inheritance, and that of characters through the sex-chromosome occurring only in one sex ($Y$ or $W$) as "one-sided" inheritance—"one-sided male inheritance" in the case of the $Y$ and "one-sided female inheritance" in the case of the $W$. Only a few instances of one-sided inheritance are known (p. 475).

The first character known to be sex-linked in plants was that of narrow rosette leaves in *Lychnis dioica*, which shows the *XY* type of sex inheritance (G. H. Shull, 1910, 1911, 1914), and is now known to have *XY* sex-chromosomes (Blackburn, 1924). In *Sphaerocarpos* C. E. Allen (1925*b*) has shown that the tendency of the spores of the quartet to remain united or to separate at maturity is transmitted through the female gametophytes only, thus paralleling the distribution of the *X*-chromosome. The cytological basis of such phenomena is obviously the same in both plants and animals.

**Evidence from Chromosome Aberrations.**—The chromosome interpretation of sex and sex-linkage has received corroboration in a number of instances of aberrant chromosome behavior. For example, in a certain strain of *Drosophila* Bridges observed the appearance of a number of types not expected from the crosses made between red-eyed males and white-eyed females. Most of the offspring were red-eyed females and white-eyed males as expected, but a very small percentage of them were white-eyed females and red-eyed males. A long series of tests showed that these results could be accounted for if it were assumed that in the original white-eyed female both of the *X*-chromosomes passed together to one pole in the first meiotic division instead of separating as they should (Fig. 202). As a result of this non-disjunction the eggs, instead of having the normal single *X*-chromosome, would have either two or none, and the distribution of the sexes and the sex-linked characters would be altered in the manner observed. In a cytological examination of the flies in which such abnormal phenomena appear, Bridges found that non-disjunction of the $X$-chromosomes does occur occasionally in the female (Fig. 203). In one line of *Drosophila* showing such a reversal of the usual criss-cross inheritance of sex-linked characters, L. V. Morgan (1922, 1925) found that the two $X$-chromosomes of the mother were actually joined together to form a single V-shaped body. Mavor (1921, 1922, 1923*a*) has shown that the non-disjunction of the $X$-chromosomes in female *Drosophilæ*, with the expected effect on sex and sex-linked characters, can be artificially induced by subjecting the flies to the action of X-rays. According to E. G. Anderson (1924*c*), the genetic data indicate a twenty-fold increase in the frequency of primary[1]

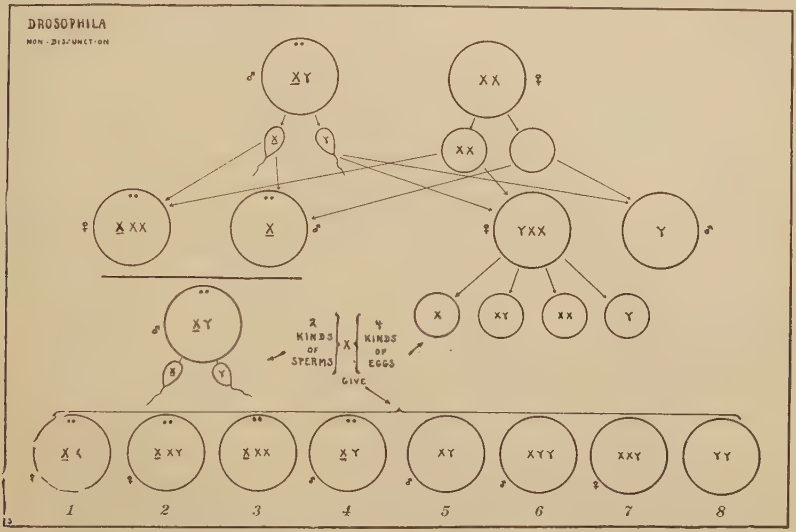

FIG. 202.—Non-disjunction and its results in *Drosophila*. The two large circles in first row represent male and female flies producing sperms and eggs respectively. Non-disjunction in the females gives 2 kinds of eggs, with $XX$ and with no sex-chromosomes, instead of the normal single kind with one $X$. At fertilization there are possible 4 combinations rather than 2, as shown in the large circles of second row. Owing to the several ways in which her 3 sex-chromosomes may be distributed at maturation, the female represented by the third circle produces 4 kinds of eggs. When mated to a normal male (below horizontal line) with his 2 kinds of sperms, 8 combinations are possible (last row). Nos. 1, 4, and 5 are normal flies and give the usual types of progeny. Nos. 2, 6, and 7, owing to the presence of 3 sex-chromosomes, give exceptional results when bred. Types No. 3 and No. 8 do not appear in the cultures, probably because they die very early. The original male has red eyes and the original female white eyes. Red eyes (represented by dots) appear in every fly bearing the $X$-chromosome of the original male, as in Fig. 201. Compare Morgan 1919*a*, Figs. 93 and 94. (*Diagram based on data of Bridges and Morgan.*)

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[1] Non-disjunction of the two $X$-chromosomes in a normal female is called "primary" non-disjunction; the separation of $XX$ from $Y$, or $XY$ from $X$, in an $XXY$ female is called "secondary" non-disjunction. Non-disjunction is also termed "reductional" or "equational" according as it occurs in a disjunctional or an equational meiotic division.

non-disjunction as a result of such treatment. In all such cases it is evident that "an abnormal distribution of the sex-chromosomes goes hand in hand with an abnormal distribution of all sex-linked factors." (T. H. Morgan).

Other disturbances in linkage relations may be due to temporary associations of non-homologous chromosomes, and also to fragmentation of chromosomes bearing linked genes. Castle (1921*b*) observed in rabbits that certain factors showed linkage in some individuals but not in others. The results could be explained on the assumption that non-homologous chromosomes were joined in the former case but not in the latter, a hypothesis which appears plausible in view of the variation in chromosome number reported for the rabbit, and the temporary associations known to occur in other organisms. The occasional coherence of two gemini has been observed, for example, in *Pentstemon* (Winge, 1925) and *Zea* (Randolph). The temporary fragmentation of chromosomes with an independent behavior on the part of the fragments would give unexpected linkage data.

**Linkage Groups.**—An extensive series of studies on linkage relations in various plants and animals has brought out the fact that the Mendelian characters of a given organism fall into a certain number of "linkage groups," the members of each group being linked to one another in various degrees, but showing no linkage with the members of other groups. It appears further, when the relationships of enough characters have been worked out, that the number of linkage groups is the same as that of the chromosome pairs. For example, *Drosophila melanogaster*, in which linkage relations have been most fully analyzed, has four pairs of chromosomes (Fig. 203): pair I is rod-shaped, pairs II and III are long and bent, and pair IV is very small. The Mendelian characters in this species fall into four linkage groups, and it is noteworthy that one of these groups comprises only three known characters. Each chromosome pair thus seems to affect a certain group of characters. It has been shown above that the main factors for one of these groups (the sexual and

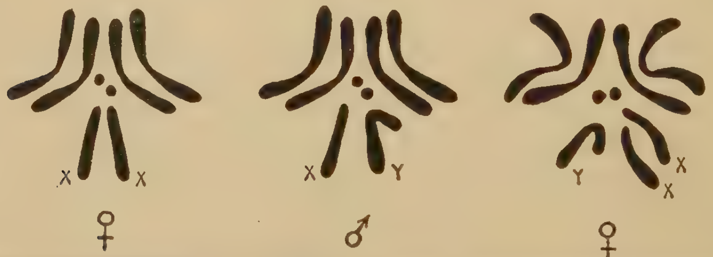

FIG. 203.—The chromosomes of *Drosophila melanogaster* as they appear during mitosis in a female, a male, and a non-disjunctional female. (*After Morgan.*)

sex-linked characters) can be definitely assigned to pair I. It is also known that the factors of the small linkage group are in pair IV. The two remaining groups, with many factors each, are assigned to the large pairs II and III. In *Drosophila Willistoni* there are three chromosome pairs and three linkage groups (Metz); in *D. obscura* there are five pairs and five groups (Lancefield 1922, 1924); in *D. virilis* there are six pairs and five known groups. Each chromosome is accordingly regarded as a body containing factors or genes affecting a considerable number of characters; and on the basis of the evidence to be presented below it is concluded that these genes, differing thus in their hereditary potencies, are arranged in the chromosome in a linear series as suggested by Roux many years ago.

In plants, linkage has been detected in a considerable number of species, but in comparatively few have more than one or two linkage groups as yet been identified, and in no case other than that of sex-linked characters can any group be referred to a distinguishable chromosome pair. Researches now in progress, however, will undoubtedly lead to marked advances in our knowledge of these matters. At present, linkage groups are best known in *Zea*, *Pisum*, and *Primula*. In *Zea Mays* there are usually ten pairs of chromosomes, and Emerson and his associates have definitely identified eight of the ten groups which seem to be present. In *Pisum*, which has seven pairs of chromosomes, five linkage groups have been identified, and since as many as seven independently inherited characters are known one may expect the discovery of linkages necessary to the identification of the two remaining groups. It is an interesting fact that Mendel, in his classic researches on *Pisum*, happened to select for special study seven pairs of characters now known to belong to as many different linkage groups, and so did not detect the phenomenon of linkage. In *Primula*, finally, two linkage groups have been identified, one of them comprising four characters and the other two. No case is known in which the number of groups exceeds the number of chromosome pairs.

Further consideration of the phenomena described in the foregoing paragraphs leads into the intricacies of one of the central problems of modern cytology and genetics. If two homologous chromosomes, each carrying factors for a certain group of linked characters (those of one group allelomorphic to those of the other group), pass into different gametes (or spores) as a result of disjunction, how does it happen that occasionally an individual transmits to a single son or daughter some of the factors of each group? If a single chromosome thus carries a series of factors for a certain group of characters, how shall one account for the offspring inheriting from one parent some of these characters but not the rest? To state the question in terms of linkage, if each group of linked characters is represented by a series of genes in a given chromosome, how is the linkage broken in a certain percentage of cases, with the resulting formation of new linkage groups, as shown, for example, by the appearance of the exceptional red-yellow and white-gray flies in the experiment cited at page 463? What is the cytological mechanism involved in this "crossing-over" or exchange of inheritance units between homologous chromosomes? Several solutions to this problem have been suggested. Among these the best known, and at present the most plausible, is that based in the *Theory of Chiasmatypy* proposed by Janssens (1909); and more recently Prell (1921, 1923*a*) has put forward another suggestion in his *Theory of Rhegmatypy*, which may prove of service in connection with certain problematic cases. The cytological phenomena involved in these theories have been described in Chapter XIII, and if they are not thoroughly well in mind the section on the Nature of the Synaptic Union (p. 282) should be reread at this point.

**Chiasmatypy and Linkage.**—According to the chiasmatype theory, the two homologous chromosomes, at some stage in the prophase of the first meiotic mitosis, may undergo a breaking and fusion at one or more points in such a way that each of the two chromosomes which separate in the anaphase is made up of one or more portions of each of the original synaptic mates (Figs. 124, 125). The two homologous chromosomes behave as usual thereafter, but they have new constitutions as a result of the mutual exchange of segments. It is this process which is supposed to be largely responsible for the breaks in linkage observed occasionally among the factors of a single group. New character groupings are thought to arise not only through crossing and ordinary Mendelian recombination, but also as a result of the formation of new groups of linked factors through chiasmatypy. As a simple illustration may be cited the following case (Fig. 204).

Crosses are made between flies with yellow bodies, white eyes, and miniature wings, and flies with gray bodies, red eyes, and long wings. In each hybrid individual there is a chromosome from one parent bearing influential genes for the three linked characters $Y$, $W$, and $M$, and a chromosome from the other parent with genes for the three linked characters, $G$, $R$, and $L$. The first three characters are allelomorphic to the last three respectively, and the two chromosomes are homologous.[1] Upon breeding from the females of these hybrids it is found that in the majority of cases (first column) the $F_2$ flies show the same genetic constitution as do the grandparents (with respect to these particular characters). This is taken to mean that each of the two homologous chromosomes forming the synaptic pair and disjoining in meiosis has remained intact—there has been no chiasmatypy. In a certain number of cases (second column) new groupings of the characters in question are observed in the $F_2$ flies: some have $Y$, $W$, and $L$, while others show $G$, $R$, and $M$. This is interpreted on the assumption that a break has occurred (dotted line) at a point of contact, so that some of the gametes, and hence the $F_2$ flies to which they give rise, receive a chromosome with *Y*, *W*, and *L*, while others receive *G*, *R*, and *M*. In a smaller number of cases (third column) the new combinations *YRL* and *GWM* are formed in a similar manner, the break and reunion occurring at another point. In a very small number of cases (fourth column) the combinations *YRM* and *GWL* appear, which can be explained on the basis of double chiasmatypy, as shown in the diagram. Most of the $F_2$ flies show the same combinations as their grandparents, which indicates that no chiasmatypy has occurred in the majority of the gamete-forming cells. Since there are many more $F_2$ individuals with *YWL* or *GRM* (second column) than with *YRL* or *GWM* (third column), it is believed that the distance between the genes *W* and *M* (and between *R* and *L*) in the original chromosome must be greater than that between *Y* and *W* (and between *G* and *R*), so that there is more chance for chiasmatypy to occur in the former case than in the latter. Thus if two linked characters are often separated (*i.e.*, have their linkage broken), their principal genes are thought to lie relatively far apart in the chromosome, whereas linked characters separated only rarely are supposed to have their genes located very near each other. Recombinations involving double or even more complex chiasmatypy (fourth column) would be expected very rarely. In this way the various genes

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[1] The hybrids have gray bodies, red eyes, and long wings, because $G$, $R$, and $L$ are dominant over $Y$, $W$, and $M$. (Ordinarily the genes have other designations.)

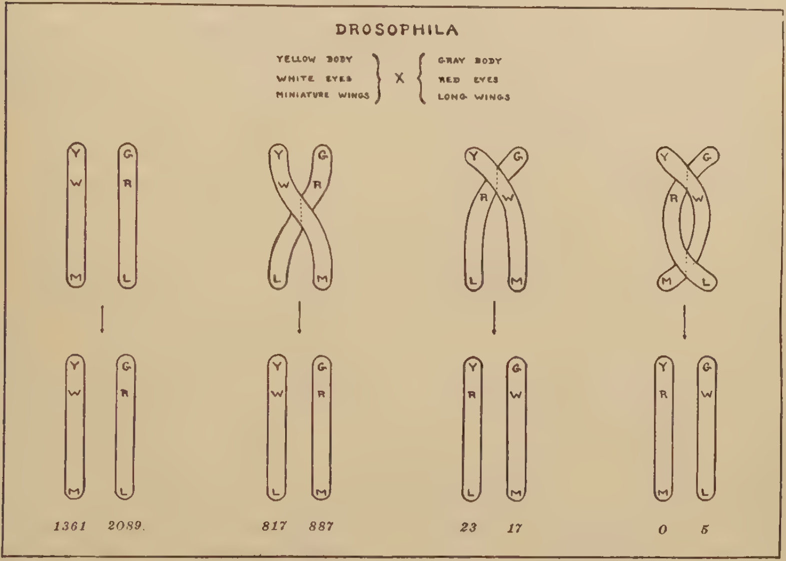

FIG. 204.—Diagram illustrating the evolution of new linkage groups through crossing-over. Explanation in text. (*Adapted from Morgan.*)

have been assigned to particular loci in the chromosomes on the basis of the frequencies in which the several new combinations in $F_2$ occur.

The linkage relations between the many genes acting in an organism may be represented in a "chromosome map" such as that being built up by Morgan and his associates for *Drosophila melanogaster* (Fig. 205). If two factors of a linked group have their linkage broken in 1 per cent of the cases (*i.e.*, if "crossing-over" occurs between them with this frequency), they are assigned to loci one unit apart in the chromosome. In chromosome II of *Drosophila melanogaster* "star" and "expanded" have their linkage broken in 4 per cent of the cases, and are placed four units apart; while "expanded" and "truncate" in a similar way are separated by five units. It is easily shown by linkage tests that this is the proper order—that "expanded" belongs between the other two. In this way it is possible to build up a map showing the linkage relations of any number of genes. Studies on other species of *Drosophila* are of much interest in this connection.[1]

It is important to note that the map distances represent the actual cross-over percentages only in the case of rather closely linked genes (10 units or less apart). Observed cross-over percentages do not exceed 50, the percentage of association shown by independently assorted genes, but the map distances may even exceed 100 units. This is because the map is built up by adding together the distances between adjacent genes, and does not take account of "double crossing-over." Between two widely separated genes two breaks may occur, with the result that these genes remain together. Taken alone they reveal no crossing-over, but examination of the linkage relations of genes between them shows that two breaks have occurred; they have, as it were, been separated and reunited. Hence for widely separated genes the map distances always exceed the observed cross-over percentages; the values given on the map indicate rather the number of breaks which occur on the average between any two genes. If there are one or three such breaks, the linkage between the two genes will be broken; if two or four, they will remain linked. It is in this way that multiple crossing-over reduces the apparent cross-over percentage. It has been found that the percentage of crossing-over differs characteristically in different chromosomes and even in different regions of the same chromosome. Hence it is impossible to give a general formula for converting map distance into cross-over percentage for all the genes; such a relation must be determined for each pair of loci independently (see Bridges, 1921*b*; Morgan *et al.*, 1922).

The relation between distance and cross-over value is further influenced by *interference*, a phenomenon elucidated by Sturtevant (1913), Weinstein

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[1] Metz (1918, 1920); Metz, Moses and Mason (1923); Lancefield (1924); Lancefield and Metz (1921, 1922); Mohr (1922); Sturtevant (1920, 1921); Weinstein (1920). For a comparison of the chromosome maps of several species, see the second citation.

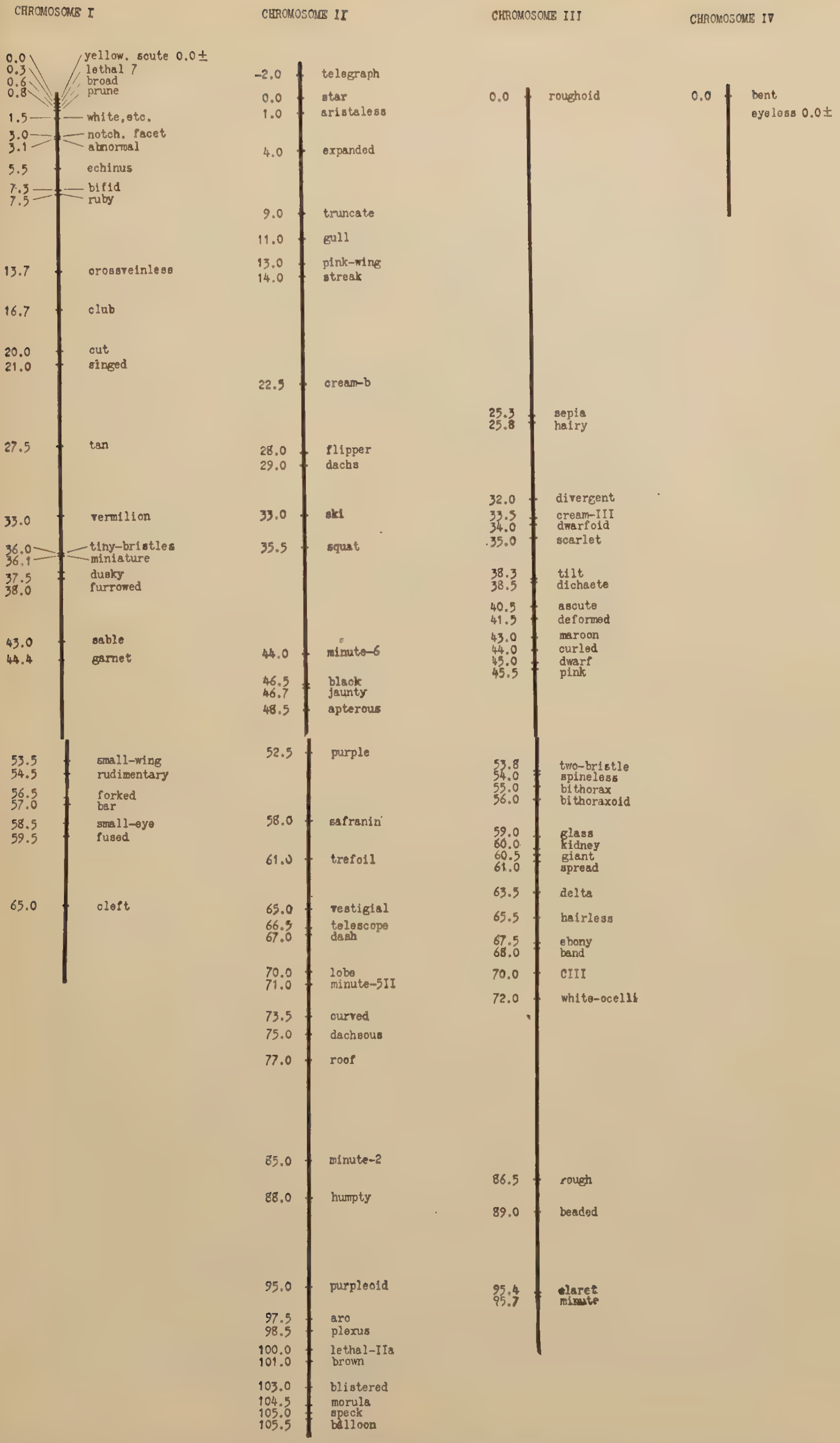

FIG. 205.—The chromosome map of *Drosophila melanogaster*, showing the loci of the genes as determined by Morgan and his associates. (*After Bridges*, 1921.)

(1918), and particularly by Muller. If the factors or genes are arranged in a linear series, it would be expected that when a chiasma occurs at a given point in a pair of chromosomes, the regions immediately on either side of this point would be prevented from forming chiasmas at the same time, as the bending of the chromosomes is not close enough to allow two chiasmas so near each other. Thus in Fig. 206, if crossing-over should occur between the two factor pairs *Dd* and *Ee*, breaking the linkages between *D* and *E* and between *d* and *e*, there would be at the same time no such break between *Cc* and *Dd* or between *Ee* and *Ff*, for mechanical reasons. Crossing-over at one point would thus interfere with crossing-over which might otherwise occur at near-by points. The amount of this interference would progressively decrease at points farther and farther from the first cross-over point, until at a certain distance (measured by the length of the loop usually formed by the bending chromosomes), as at *LM*, it would vanish entirely; here crossing-over would occur with its normal frequency irrespective of any cross-over at *DE*.

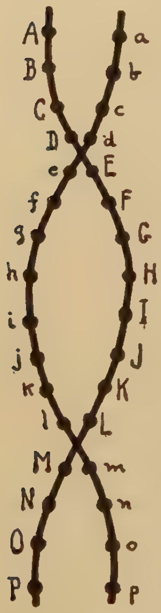

FIG. 206.—Diagram illustrating interference. Explanation in text.

Muller has found that the characters are inherited according to these expectations. If two genes have their linkage broken in a certain percentage of cases, this percentage is noticeably lowered if breaks in linkage occur between two other genes having normally a fairly close linkage with the first two. In other words, one linkage break interferes with other linkage breaks within the same linkage group, and the degree of this interference varies from a high value in the case of a closely linked series of genes to zero in the case of those very loosely linked. This, it is pointed out, is just what should occur among characters represented by a linear series of genes in chromosomes which undergo chiasmatypy, but which cannot twist about one another with more than a certain degree of closeness. Weinstein (1918) has shown that in chromosome I (*X*) of *Drosophila* the distance at which interference disappears is about 46 units, and that it reappears beyond this point, indicating a modal distance between the two breaks in double crossing-over.

The effect of external agencies on crossing-over has been investigated in a few instances. Plough (1917, 1921) found that abnormally high or low temperature has an influence on the amount of crossing-over in certain regions of chromosomes II and III of *Drosophila*, but not in chromosome I. Mavor (1923*b*) and Mavor and Svenson (1923) have shown that if females are subjected to the action of X-rays before mating, the amount of crossing-over during oögenesis is decreased for certain factors in chromosome I and increased in chromosome II. Bridges observes that the amount varies with the age of the female.

A further point regarding crossing-over is of considerable interest. In *Drosophila* it is only in the females that crossing-over occurs; new combinations resulting from this process appear in the eggs but not in the spermatozoa. This is of much importance to the working geneticist. He can rely on the production of only non-cross-over gametes by the male, which greatly simplifies his labor. The reason for the lack of crossing-over between the *X* and *Y* chromosomes probably lies in their wide functional difference, as indicated by the curious fact that the *Y* appears to have very little effect upon any characters. As pointed out in the preceding chapter, the sex of the fly is correlated with the numerical ratio of *X*-chromosomes and autosomes, rather than with the presence or absence of a *Y*. The absence of a *Y*, however, has been shown in some cases to be correlated with sterility. Certain organisms regularly have no *Y*. Although the failure of crossing-over between *X* and *Y* may possibly be thus attributed to the restricted functional state of the *Y*, it is not apparent why this failure should involve the autosomes also. In the fowl, which is digametic in the female, crossing-over is confined to the male.

Contrasted with the condition in *Drosophila* is that reported in the fishes, *Lebistes reticulatus* (Schmidt, 1920; Winge, 1922*ab*, 1923*a*) and *Aplocheilus latipes* (Aida, 1921). In *Lebistes* there are 46 chromosomes in both sexes, and sex-inheritance is of the *XY* type. The inheritance of colors confined to the males is best accounted for on the basis of dominant factors in the *Y*-chromosome: they follow the distribution of the Y-chromosome from male to male, and thus represent an instance of "one-sided male inheritance." Furthermore, one of these characters, after being so inherited for a time, has been observed to be inherited through some generations as a sex-linked character, and later in the original mode once more. This is interpreted as the result of a crossing-over between the *X* and *Y*, whereby the factors concerned are transferred from the *Y* to the *X*, and later from the *X* to the *Y* in a second crossing-over. Similar data are at hand for *Aplocheilus.* A further instance of one-sided male inheritance is reported in the case of webbed toes in man by Scofield (1921). Hence it seems clear that in some cases the *Y*-chromosome, like the *X*, carries factors affecting certain somatic characters. Genetic data indicate that in a great many organisms crossing-over regularly occurs in both sexes. It is not improbable that the various behaviors reported are correlated with degrees of functional difference between the *X* and *Y*, or between the *Z* and *W*.

**Rhegmatypy and Linkage.**—The Theory of Rhegmatypy proposed by Prell (1921, 1923; see p. 288) offers another method by which blocks of genes may be exchanged between homologous chromosomes in such a way as to account for the genetic data of crossing-over. It is supposed that the reunion of segments of chromosomes which have undergone a temporary fragmentation into two or three parts may frequently occur in such a way that new combinations of segments are formed; two homologous chromosomes may in this way exchange corresponding portions. The result of such a process would be the same as that of chiasmatypy at this point in the chromosomes, whether the chiasmatypy were of the typical kind or the "late" kind also described by Janssens. In general, however, the rôle of rhegmatypy would seem to be very restricted as compared with that of typical chiasmatypy. The former process apparently involves breaks at very few points in a chromosome, perhaps only one, whereas typical chiasmatypy evidently may take place at a large number of possible points. In the opinion of Prell, both processes probably occur, often even in the same organism. Most of the complicated data from *Drosophila* can be interpreted only on the basis of chiasmatypy occurring at many points in the chromosome; but it may be that such facts as the "deficiency" of a certain block of genes usually attributed to a loss or inactivation of a certain portion of a chromosome, as well as the "duplication" of such a block, should be attributed to rhegmatypy, or to Janssen's "late chiasmatypy." Appeal might be made to rhegmatypy to account also for crossing-over of genes in organisms not exhibiting parasynapsis. Further genetic and cytological evidence bearing on these important points is awaited with much interest.

**Discussion.**—In the foregoing pages has been given a brief account of the main points of the theories which have been developed by those who have made the most thoroughgoing attempts to relate the phenomena of heredity to some visible protoplasmic basis. To follow out in detail the application of these theories does not lie within the scope of these chapters, the purpose of which is rather to furnish a starting point for cytological studies in this field by indicating the nature of the common ground upon which cytology and genetics meet. Bearing in mind the phenomena of inheritance reviewed in this and the previous chapters, it is difficult to escape the conclusion that differential factors of some sort, which in an unknown manner initiate the series of reactions resulting in the several characters, are carried in the nucleus. To determine the nature of these factors and to discover the real relation existing between them and the developed characters are among our greatest problems. That the factors, or genes, are discrete units is a hypothesis which is not only plausible but is also proving to be exceedingly useful. If such units exist, the chromosomal mechanism affords a means of precisely the kind required to transmit them through a series of generations in the way that their corresponding characters are seen to be inherited. Hence from the time of Roux and Weismann onward the inheritance factors have been supposed to lie in the chromosomes.

Unfortunately no such units can be directly observed with the microscope. Although all workers admit that it is not at present possible to determine accurately the size which genes must have, it is of interest to note that tentative calculations place them well below the limit of visibility with the ordinary microscope, and suggest that they are of the same order of magnitude as certain protein molecules (see Morgan, 1922). Very often the chromosome reveals a highly characteristic longitudinal differentiation in the size and position of its chromomeres (Fig. 65), but it cannot yet be stated in what manner, if at all, these bodies are related to functional differentiation within the chromosome. On the basis of size and number, one would have to conclude that the chromomere must at best include a large number of genes. Whatever may be the significance of chromomeres with respect to hereditary function, one can hardly fail to recognize the highly suggestive nature of the arrangement of the chromosomal material in the form of a slender thread, the frequent evidences of longitudinal differentiation in this thread, and its division into two equal portions in mitosis, to say nothing of the remarkable disjunction of homologous chromosomes in meiosis. Although our evidence lacks the directness naturally desired, there is much to indicate a serial arrangement of "qualities" in the chromosomal thread as suggested by Roux.

With regard to chiasmatypy, which is the principal means by which the exchange of inheritance factors between homologous chromosomes is supposed to be accomplished, it may be said that the cytological evidence for its occurrence has been greatly strengthened by the work of Janssens (p. 285). The earlier figures by this investigator were interpreted in another way by certain workers, but his recent contribution strongly supports his own interpretation. It now seems very probable that through chiasmatypy, and to some extent through rhegmatypy, exchanges of chromosomal elements are brought about, with a corresponding effect on the constitution of linkage groups.

At this point it may be well to recall (see p. 283) that the synaptic threads in many cases are said to become much more closely associated throughout their length than is supposed by some advocates of the chiasmatype theory. A number of observers have reported an actual fusion of the conjugating threads, the resulting pachytène thread subsequently splitting, probably along the line of this fusion. It may accordingly be suggested, in harmony with the hypotheses discussed by C. E. Allen (1905), that if the threads actually carry or consist of discrete units, or genes, and if these units do not themselves fuse during the process, such a resplitting of the pachytène thread, if not wholly along the fusion plane because of a twist of the thread or of the plane itself, would bring about a redistribution of the genes as effectively as would the chiasmatype process as originally proposed. The splitting of chromatic threads is, moreover, a process already known to occur in all other mitoses. But interpretations involving the actual fusion of the conjugating threads have been adversely criticized, and only further research can lead to an adequate evaluation of the above outlined suggestion. The problem of genes can be better dealt with after the behavior of chromosome segments and chromosomes as wholes throughout the nuclear cycle has been more fully analyzed.

## CHAPTER XXI

## WEISMANNISM AND OTHER THEORIES

The theory of heredity described in the foregoing chapters, though resting on its own foundation of observational and experimental evidence, shows in some of its features the influence of certain earlier speculative hypotheses, particularly those set forth by August Weismann.[1] Some of the conceptions embodied in these hypotheses form the background of many cytological and genetical discussions of the present day, and for this reason their main points will here be outlined.

Although conceptions of other types arose very early, many of the hypotheses in question were based on the assumption that the phenomena of heredity and development are the result of the activity of ultimate living particles of ultra-microscopic size. Thus Herbert Spencer (1864) built up a theory of considerable proportions about his "physiological units," and these formed the prototype of the units postulated in many later theories. Of such speculations the most influential were those of Darwin, Nägeli, de Vries, and Weismann.

**Darwin's Hypothesis of Pangenesis.**—In his *Variations of Plants and Animals under Domestication* (1868) Darwin included a chapter on his "Provisional Hypothesis of Pangenesis," which, though offered only as a suggestion, excited great interest in the field of biology, especially after the advances made in cytology a few years later. In several points it closely resembled a theory propounded by Buffon more than a century earlier (1749). Darwin clearly saw in the cytological aspects of heredity one of the great biological problems of the future, but his only speculations on the subject were embodied in the pangenesis hypothesis, which may be stated as follows.

All the cells of the organism at all stages of development give off small particles, or *gemmules*, which multiply by fission and circulate throughout all parts of the body. These gemmules pass to the germ cells, carrying with them the power to reproduce cells like those from which they came. In this way units representing all the kinds of cells present in the organism are collected in the gametes (or spores or buds) and are thus passed on to the next generation. During the embryogeny the gemmules are so distributed that at the proper times and places they develop into cells like those from which they originally migrated, in this manner building up a new individual like the parent. Some of the gemmules do not function until a comparatively late stage in the ontogeny, and others may remain latent through several generations; on these two assumptions it is possible to account for the late appearance of certain characters, and for the fact that others may "skip" one or more generations. It is further supposed that some gemmules remain latent in the individuals of one sex; thus the characters normally present only in the male may be transmitted through the female.

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[1] See Kellogg (1907), Delage and Goldsmith (1913), Thomson (1899, 1913), and Conklin (1915).

In the many criticisms of this hypothesis the tendency has been to judge and condemn it solely on the ground of the supposed transportation of the gemmules from the body cells to the germ cells, for which no direct evidence has ever been discovered. It should not be forgotten, however, that Darwin suggested an explanation for the phenomena of heredity on the basis of representative material units in the cells, a conception which was of the greatest importance in that it constituted the starting point for later fruitful investigations and theories. The migration of the gemmules was postulated largely to account for regeneration and the inheritance of acquired somatic modifications. Since regeneration may be explained as well on other grounds, and since the evidence for the inheritance of acquired somatic modifications is for the most part of such extremely doubtful value, such a migration of representative units, first denied by Galton (1875), has come to be regarded as unnecessary. A theory postulating representative particles but no such migration was that of de Vries.

**De Vries's Theory of Intracellular Pangenesis.**—According to de Vries (1889), the particles of hereditary substance, or *pangens*, do not represent different kinds of cells, as Darwin thought, but stand rather for different elementary characters, or qualities, out of which the many visible characters of the organism are built up. Furthermore, these living elements, or pangens, do not pass from cell to cell, but merely circulate between the nucleus, where a complete outfit of them is conserved, and the cytoplasm—hence the term "intracellular pangenesis." In this way the pangens brought into the new individual through the nucleus influence the character of the cell as a whole. Contrary to the idea of Darwin, and especially that of Weismann (see below), all the cells (or nuclei) of the body contain pangens for all the hereditary characters; they are not sorted out as development proceeds.

**Nägeli's Idioplasm Theory.**—A highly speculative theory of a somewhat different type was that formulated by Nägeli (1884) five years before that of de Vries. Protoplasm was thought by Nägeli to be made up of a vast number of fundamental units; these he called *micellæ*. As a result of the ways in which these molecular complexes, or micellæ, may be arranged, there are in the cell two kinds of protoplasm: in nutritive protoplasm, or *trophoplasm,* the micellæ have no regular orientation, whereas in *idioplasm* they are oriented in a particular manner. According to Nägeli, the phenomena of heredity are due to the constitution and transmission of this idioplasm; idioplasm is the physical basis of heredity. It is not confined to the nucleus, but forms an elaborately constituted network extending throughout all parts of the organism. By arranging themselves in various groupings within this network, the micellæ are able to bring about the development of the many specific characters. The further details of this highly "fragile" hypothesis are summarized in convenient form by Delage and Goldsmith (1913), who point out that in spite of its many unsupported assumptions it did involve two fertile ideas: first, that there are two kinds of protoplasm, one of which carries something peculiarly responsible for inherited characters; and, second, that there are a limited number of elementary characters which combine in various ways to produce the many visible characters.

**Weismann's Theory.**—The most highly developed of all such speculative theories was that of Weismann. On the basis of the general conception of pangens Weismann built up the highly involved system of hypotheses set forth in his *Das Keimplasma* (1892) and in more elaborated form in his *Vorträge über Deszendenztheorie* (1902). Certain modifications were later made.

As Delage and Goldsmith have noted, Weismann incorporated in his theory several of the stronger points of earlier theories, such as Darwin's conception of representative particles, Nägeli's elementary characters, and de Vries's intracellular migration of particles. With Nägeli he distinguished between nutritive *morphoplasm* and hereditary *idioplasm,* or *germ-plasm,* but unlike Nägeli he identified the latter with the chromatic substance of the nucleus.

*The Germ-plasm.*—Weismann's conception of the constitution of the germ-plasm was essentially as follows. The ultimate unit in all living matter is the *biophore,* which is a minute living particle capable of growth and reproduction. The many kinds of biophores in a given cell represent the many characters of that individual cell. They are not bearers of the characters as such (though Weismann often spoke of them in this fashion), but are rather factors upon whose presence the development of the characters depends. The biophores are grouped to form units of a higher order, known as *determinants.* The determinant, since it is composed of the many kinds of biophores in the cell, has the power of determining the development of a certain type of cell or group of cells. In general, therefore, there are as many sorts of determinants in the organism as there are types of cells, or "independently variable parts."

The determinants are, in turn, grouped into *ids.* A single id contains all the kinds of determinants, and so stands for the sum of all the characters of the organism; it contains the "complete architecture" of the germ-plasm. The ids in a given species differ only slightly among themselves, the differences corresponding to the variations observed within the species; they are the "ancestral germ-plasms" contributed by past generations. The ids are identified with the visible chromatic granules in the nuclear reticulum or in the chromatic thread during mitosis. In most cases the ids are grouped to form *idants,* or chromosomes. In some species which have a large number of granular chromosomes it is possible that each is composed of but one id. The id, therefore, rather than the chromosome, is the unit of primary importance. In case there are several ids in a chromosome, they are arranged in a linear series. The idea that the chromosomes are all alike because they carry closely similar ids was later modified by Weismann (1913), largely as the result of the demonstration that very minute character differences are segregated in Mendelian fashion.

It has been pointed out (p. 251) how Weismann supposed the summation of ids to be prevented by periodic "reducing divisions." These he thought might involve either a transverse division of the chromosome instead of the ordinary longitudinal division, or the elimination of entire chromosomes.

*Ontogenesis.*—With the aid of this elaborate mechanism Weismann explained ontogenetic development in the following manner. In the zygote from which the individual is to develop, all the kinds of determinants are present: those of the female parent were contained in the egg nucleus and those of the male parent were brought in by the nucleus of the spermatozoön. During the long series of nuclear divisions beginning with that in the zygote and ending with the completion of the mature organism, the many kinds of determinants are sorted out through a progressive disintegration of the ids, and are distributed in a definite and orderly manner to the different parts of the body. Many somatic mitoses are therefore regarded not as equational (*erbgleich*), but in reality qualitative (*erbungleich*). When a given determinant finally reaches the proper cell, *i.e.,* when that cell is finally formed, the determinant splits up into its constituent biophores, and these, through their action on the protoplasm, give to the cell its specific characters. The general character of a cell is accordingly due to the type or types of determinant which it receives. For Weismann, therefore, development (ontogenesis) was definitely bound up with the evolution or unfolding of a complex structure contained in the zygote. Although he did not hold that the units in the zygote have the same spatial relations as their corresponding characters or structures in the adult, it has been said with some degree of truth that he transferred preformationism to the nucleus.

*Heredity.*—Such being Weismann's conception of development, how did he account for heredity? If the various kinds of body cells in an individual are characterized by different types of determinants, how is it that the germ cells, or gametes and zygote through which this individual is to give rise to the next generation, possess complete outfits of determinants? According to Darwin's hypothesis, outlined above, representative particles, or gemmules, are contributed by all parts of the body at all stages to the germ cells, by which they are transmitted to the next generation (Fig. 207, *A*). Such a contribution of elements from the body cells to the germ cells was denied by Weismann. He held rather that a certain portion of the complete germ-plasm of the zygote is carried along

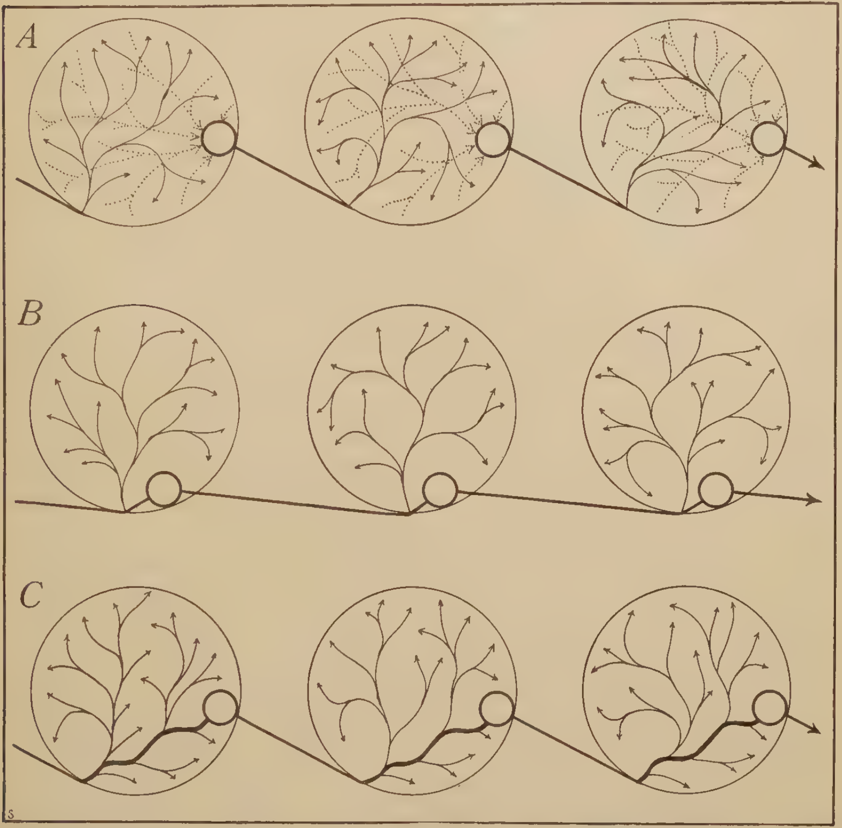

FIG. 207.—Diagram illustrating the hypotheses of Darwin and Weismann. The large circles represent successive generations of individuals, and the small circles their germ cells. For the sake of simplicity inheritance is shown as uniparental rather than biparental. *A*, Darwin's Hypothesis of Pangenesis. The branching solid lines ending in arrows represent the sorting out of the hereditary units (gemmules) during ontogenesis; the dotted arrows show the migration of gemmules from the body cells to the germ cells, by which they are carried into the next generation. *B*, *C*, Weismann's theory of the continuity of the germ-plasm, with no contribution of hereditary units from the body cells to the germ cells. In one case (*B*) the germ cells are set aside at the beginning of ontogenesis, and in the other (*C*) much later. In both cases the "complete germ-plasm" is delivered to the germ cells through a shorter or longer series of equational divisions (heavy lines).

unchanged and delivered intact to the germ cells. It had been shown that in certain animals the primitive germ cells are set aside at once when development begins, and Weismann pointed out that they are therefore differentiated before any sorting out of the hereditary units can have taken place. Hence the germ cells are really produced by the germ cells of the previous generation and not by the individual's own soma (body); they are present from the beginning of development with the full hereditary outfit, and by a few equational divisions they give rise to the gametes. This is represented in Fig. 207, *B*. In the case of those animals and plants whose germ cells appear later in the ontogeny Weismann held that, although a sorting out of the units occurs in the majority of the cells during ontogenesis, those meristematic cells which constitute the chain connecting the zygote with the germ cells—the *germ-track* (*Keimbahn*)—maintain the undiminished germ-plasm (Fig. 207, *C*). Hence in all cases there is a continuity of the germ-plasm, if not a continuity of the germ cells (unless meristematic cells also are regarded as germ cells). Since the germ-plasm of any generation is derived directly from that of the preceding one, it is continuous through an unlimited number of generations; and the successive somas (bodies) are, so to speak, side branches given off at intervals from the main stream of the germ-plasm.

*Origin of Heritable Variations.*—In elaborating the above views Weismann (1885, 1892) insisted strongly upon the independence of the "potentially immortal" germ-plasm and the transient and mortal soma. He argued that since there is no contribution of hereditary elements from the soma to the germ cells, somatic changes being in no way impressed upon the germ cells from which the next generation is to arise, there can be no inheritance of acquired somatic modifications. In multicellular animals the only inherited variations are those originating in the germ-plasm of the germ cells or germ-track as responses to internal (nutritive, etc.) or external environmental stimuli, and those due to recombinations of hereditary units at the time of syngamy (amphimixis). Weismann admitted that the germ-plasm, though remarkably stable, might be altered directly by the environment (parallel modification of germ and soma), or even by modifications in the surrounding soma; but he denied that in the latter case the alteration would be of such a nature as to cause the reappearance of the same somatic modifications in the next generation. He attempted to show how it is that the stream of germ-plasm on the one hand maintains a stability sufficient to account for the resemblance between the successive bodies springing from it at intervals, and on the other hand undergoes orderly changes responsible for the evolutionary advance shown in a long series of generations. In the words of Agar, "according to Darwin, parents truly *transmit* their characteristics to their offspring (by means of gemmules). According to the modern view [Mendel; Galton; Weismann], however, children resemble their parents not, strictly speaking, because the latter have passed something on to them, but because both have been produced from the same germ-plasm"(Bower, Kerr, and Agar, 1919). "The parent is rather the trustee of the germ-plasm than the producer of the child" (Thomson, 1913).

Weismann accounted for the internally induced heritable variations on the basis of his theory of *Germinal Selection.* He supposed that the determinants, while multiplying in the germ cells, are subject to selection like all other organic units. Some determinants, being better placed with respect to nutritive conditions, are favored thereby and grow stronger and more influential, while others undergo changes in the opposite direction. The parts of the organism receiving the determinants which have had the advantage in the struggle become better developed than those receiving the weaker determinants. As this process continues from generation to generation the new variation gradually increases until it becomes pronounced enough to be laid hold of by natural selection. In this manner Weismann accounted for the preservation of small variations not yet of selective value, and for continued variation along definite lines (orthogenesis) in both plus and minus directions. Thus for him selection was the cardinal principle which ruled not only over organisms, but also over cells, ids, determinants, and biophores. As he himself stated it, "this extension of the principle of selection to all grades of vital units is the characteristic feature of my theories."

**Modern Aspects of Weismannism.**—In the foregoing sketch of Weismann's theory a number of approaches to more modern conceptions may be recognized. A brief comparison will help to make this clear.

*The Germ-plasm.*—The term "germ-plasm" is at present used in two senses. Since development and heredity obviously involve the action of a protoplasmic system made up of nuclear and cytoplasmic components, germ-plasm in the broad sense may be regarded as any protoplasm capable, under the proper conditions, of developing into an individual and reproducing its kind. This practically identifies the germ-plasm with the complete protoplasmic system, and so renders the former term superfluous. The geneticist, however, finds the term useful in a narrower sense. It has been shown that the phenomena of heredity are closely correlated with the activity of a nuclear mechanism. This mechanism seems to consist essentially of a system of chromosomal materials or units having a highly differential effect on the development and inheritance of specific characters. Although recognizing that such phenomena represent or depend on functions of the protoplasmic system as a whole, the geneticist often finds it convenient to deal separately with the nuclear substance more especially differentiated in connection with the hereditary function under the name of germ-plasm. It is in this special sense that the term is used in the present discussion.

In their conception of the nature of the units of inheritance, geneticists have departed rather widely from Weismann. For him each of the ids arranged in a series in the chromosome represented the sum of the characteristics of a complete organism; the smaller parts of the body were represented by the smaller units (determinants) composing the ids, and these units in turn were made up of ultimate living biophores. The gene of today, on the contrary, stands neither for a complete organism nor for any constituent part thereof; it is conceived rather as a mass of some chemical substance which acts together with other genes in affecting many processes and hence characters in various parts of the organism. Genes are not simply the "determiners" of characters, but are rather constitutional factors influencing the course of developmental processes, which are also affected in various degrees by environmental agencies. The lack of a certain character may be correlated with the absence of a particular gene, but this does not mean that this gene, when present, is alone responsible for the character; it indicates only that the gene is a particularly important element of a system whose total action results in the development of the character (see p. 375).

With regard to the frequent statement that Weismann's theory was fundamentally a vitalistic one, it may be pointed out that, although the biophores were regarded as living units, Weismann stated that "they are not composed in their turn of living particles, but only of molecules, whose chemical constitution, combination, and arrangement are such as to give rise to the phenomena of life." He urged that, although it cannot be proved that no peculiar vitalistic principle exists, one should hold fast to a purely physico-chemical basis of life "until it is shown that it is not sufficient to explain the facts, thus following the fundamental rule that natural science must not assume unknown forces until the known ones are *proved* insufficient."

The view of Roux and Weismann that the inheritance units are arranged in a serial order in the chromosome is receiving striking confirmation in the modern genetic analysis of the rôle of chromosomes. Cytological researches are also showing that the chromosome has a longitudinally differentiated structure, though it is not at present possible to relate this differentiation very closely to the functional differentiation which seems to exist. Allusion has been made to the fact that Weismann discarded his original assumption that the chromosomes of the complement are essentially alike in favor of the view that they are characteristically different, as has been known since the work of Boveri. The reduction of the number of units postulated by Weismann has been found to occur, and at just the stage of the life cycle predicted by him, but it is not accomplished in the manner he thought probable.

*Ontogenesis.*—Weismann's theory that ontogenetic differentiation is due primarily to a sorting out of unlike units of the germ-plasm representing different body parts has been abandoned in favor of the view that all the nuclei of the body retain descendants of all the inheritance factors present in the original zygote nucleus. In the first place, no cytological evidence for such a sorting out has been discovered; the chromosomes are equationally divided in every somatic mitosis throughout development, so far as one can see. To this objection Weismann had only to reply that the units sorted out are invisible determinants rather than ids or idants, so that visible differences would not necessarily arise in the chromosomes. A second objection to the theory was pointed out in the phenomenon of regeneration, whereby differentiated body cells may under appropriate conditions give rise to a complete new individual with functional germ cells. For this Weismann formulated an additional hypothesis, stating that during the differential distribution of the units certain "supplementary determinants" are carried along unaltered, and that later, if occasion arises, these cause the development of a complete organism. Such an explanation, however, scarcely seems convincing in view of the increasing number of cases in which differentiated cells are shown experimentally to retain the developmental capacities of their undifferentiated forerunners.

Especially instructive in this connection are the results of experiments on developing animal embryos.[1] For example, it has been observed that if one of the two blastomeres formed by the cleavage of the frog's egg be injured, the uninjured blastomere produces a half-embryo; but if the injured one be removed, the other may produce a whole. Moreover, it now seems clear that the development of an isolated blastomere into a half or into a whole depends on whether or not the plane of the cleavage separating it from its sister coincides with the median plane of the future embryo, which is in some way determined in the egg cytoplasm before cleavage. In other words, differentiation may be well on its way before nuclear division begins. Again, the relative position of cells in the embryo may be artificially altered, whereupon the cells develop into structures proper to their new locations rather than into those of the regions from which they came. Brachet observed cases in which supernumerary male nuclei in the egg divided and gave rise to cells which were incorporated as integral parts of the embryo with no dislocation of development. Such phenomena suffice to show that the pattern of the embryo, the behavior of different blastomeres, and the latter course of differentiation cannot be simply the result of a differentiation of the nuclei as Weismann supposed. Certain structures arise in certain regions of the embryo irrespective of what particular nuclei happen to be present there (*cf.* p. 490).

Ontogenesis should be regarded as an act of the protoplasmic system as a whole, and not merely as the result of the action of its inheritance units alone. As the organism grows, its nuclei multiply by equational divisions, so that all parts of the body contain the same type of nuclear mechanism, or complex of genes. The kinds of reactions which can occur in the growing mass, and hence the characters which develop, are largely conditioned by the type of gene complex present, but different portions of the organism differentiate in various ways because of the different conditions inevitably arising in such portions of a growing mass. Differentiation in the body does not indicate a parallel differentiation of the gene complex, but rather the capacity of protoplasm with a given gene complex for varied but harmonious reaction to the many local conditions

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[1] See Brachet (1916), Conklin (1924), Morgan (1924*e*).

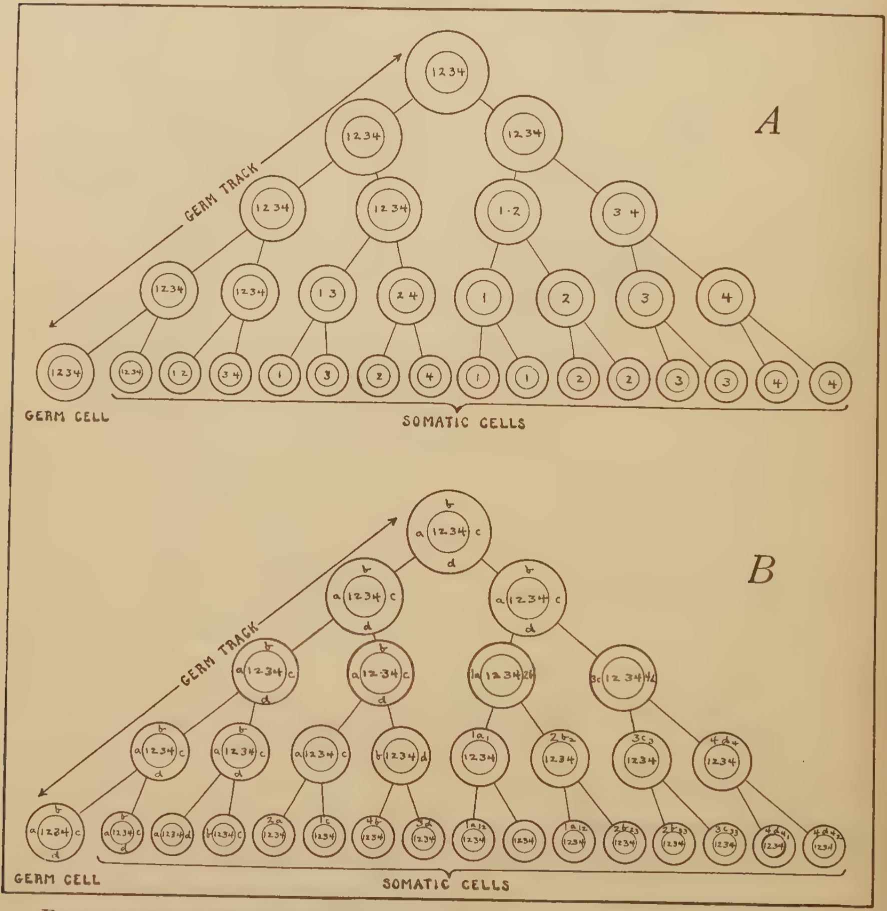

FIG. 208.—The behavior of the hereditary units in ontogenesis, according to Weismann (*A*) and the current interpretation (*B*). In *A* the determinants in the nucleus (1, 2, 3, 4) are supposed to be distributed differentially to the various somatic cells. In *B* the genes (1, 2, 3, 4) are distributed equally to every cell, but the cytoplasm is distributed differentially. The same genes working upon different cytoplasms produce different results in various somatic cells. (*Diagrams and legend from Conklin*, 1919–1920.)

arising as development proceeds. In harmony with this interpretation is the fact that it is in the cytoplasm rather than in the nucleus that most protoplasmic differentiation is manifested (see Fig. 208).

Almost nothing is known concerning the means by which the gene system produces its effects upon differentiation. The Mendelian theory has so far been concerned with heredity rather than development. It represents primarily an attempt to account for the initial resemblances or differences in hereditary potentiality which are observed to exist between the germ cells from which successive generations arise. Between the gene system present at the beginning of ontogenesis and the expressed characters of the organism "lies the whole world of embryonic development." At all stages nucleo-cytoplasmic interchanges play a fundamental rôle, but just how these involve the genes can at present only be conjectured. "In what way and at what times the nuclear materials take part in the determination of characters we do not know. The essential point is that we are in no way committed to any interpretation. Stated negatively we might add that there is nothing known at present to preclude the possibility that the influence is a purely chemical process" (Morgan, 1920*b*).

It is clear that the methods and results of development are definitely correlated with an inherited constitution. But such a conception need involve neither the crude preformationism of the early days of biology, nor the unfolding of a germinal mechanism postulated by Weismann. In any case it is to be remembered that the action of the organism, like that of any other mechanism, is really the action of a larger system of which organism and environment are integral parts, and that the action may in a certain measure be controlled through either of these parts (*cf.* p. 455).

*Heredity.*—Weismann's theory that heredity is conditioned primarily by the genetic continuity of the germ-plasm has been well substantiated; the preservation of a specific type of nuclear organization through successive generations by growth and division lies at the very basis of our modern theory. But the idea that this organization is maintained only in germ cells sharply distinct from the somatic cells has been found to be inadequate. It is true, as has already been stated, that in many animals the reproductive cells are differentiated from the body cells very early in the course of ontogenesis, but present-day views differ markedly from Weismann's with respect to the rôle of the nuclei in this process.

In *Ascaris megalocephala* the germ cell line (germ-track; Keimbahn) can be distinguished from the time of the first cleavage of the egg: the primitive germ cell is definitely set apart at the fourth cleavage division and thereafter gives rise to a distinct group of germ cells. The behavior of the chromosomes during these early divisions is very peculiar. At each mitosis beginning with the second (Fig. 209) the chromosomes in the somatic cells become subdivided into smaller pieces and lose their ends in the cytoplasm, while in the cells of the germ-track they remain entire (Boveri, 1887*c*, 1889, 1891, 1892, 1904; Zacharias, 1913). Such a "chromatin diminution" in somatic cells has also been observed in a few other cases (*e.g.*, *Miastor*: Kahle, 1908; Hegner, 1912, 1914). It appears significant for the chromosome theory of heredity that the reproductive cells should be the ones to receive the "undiminished germ-plasm," but that the diminution in the somatic cells indicates such a sorting out of units as Weismann held responsible for differentiation is no longer a tenable view. This process occurs in comparatively few organisms; and although its significance is obscure, it now seems clear that it is a result, rather than the cause, of protoplasmic differentiation (Boveri, 1910).

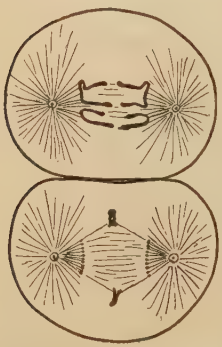
FIG. 209.—Chromatin diminution in second cleavage mitosis in *Ascaris*. (*After Boveri.*)

That a distinction between germ cells and body cells in such cases is not to be made on the basis of differences in their nuclei is shown by phenomena in the embryogeny of certain insects. Here the protoplasm which is to constitute the future germ cells can be distinguished very early, even in the unsegmented egg, either as a visibly differentiated region in the cytoplasm at one pole of the elongated egg (Fig. 210), or by the presence of certain inclusions known as "Keimbahn determinants," or "germ cell determinants."[1] Such eggs often undergo a period of free-nuclear division before cleavage into cells begins, and it is observed that any nucleus which happens to come into the differentiated polar protoplasm may become a germ cell nucleus (Huettner, 1923, on *Drosophila*). Hence the development of germ cells is due to a differentiation taking place in the developing egg as a whole, and not to a distinction between the various nuclei, all of which seem to possess the capacity for functioning as germinal nuclei. This is very different from the idea of Weismann. (In passing it may be pointed out that the phenomena mentioned here afford substantial support to the organismal theory of development, which was emphasized in Chapter III, and which is not necessarily less factorial than the cell theory.)

In other groups of animals it has been found that the germ cells may be differentiated at various periods, often very early, but there is an abundance of evidence to show that this does not involve an irreversible differentiation of developmental capacities. Many cells already undergoing somatic specialization may dedifferentiate and become specialized in other ways, even as germ cells. Frequently the first formed germ cells degenerate, the functioning ones arising later from developing somatic tissues. In certain lower animals the somatic tissues retain this power of dedifferentiation indefinitely, whereas in higher forms specialization

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[1] These terms are misleading, for the bodies in question are not known to have any causal relation to the differentiation of the germ cells. For a discussion of this subject, see Hegner (1914).

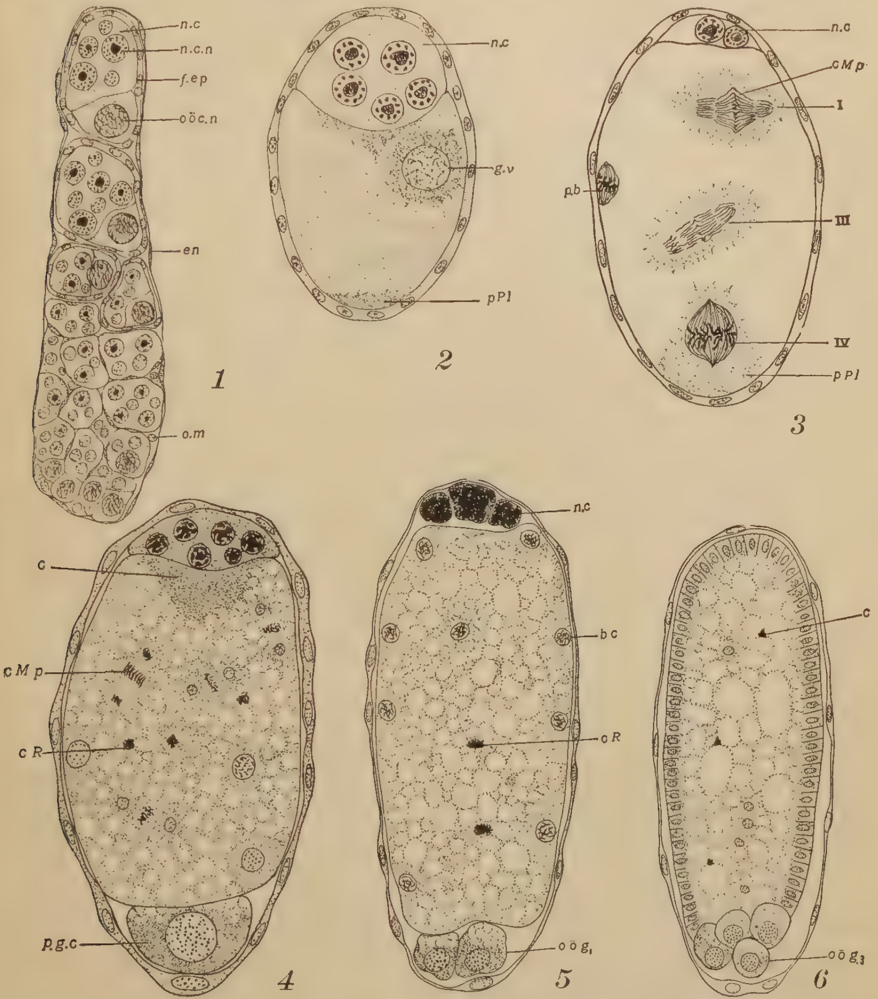

Fig. 210.—Oögenesis and early embryogeny in *Miastor*. 1, longitudinal section through ovary: *f. ep*, follicular epithelium; *n. c*, nurse chamber with several nuclei; *oöc. n*, oöcyte nucleus. 2, oöcyte nearly full-grown: *g. v*, germinal vesicle; *pPl*, pole-plasm. 3, third embryonal mitosis, showing three of the four figures; the small figure at the left is a dividing polar body. The pole-plasm is being provided with a nucleus. 4, pole-plasm with its nucleus cut off as primordial germ-cell; nuclei in main portion of embryo continuing to divide freely. 5, the primordial germ-cell has divided to form two oögonia; somatic portion of embryo still in cœnocytic condition. 6, eight oögonia present, four of them shown; embryonic protoplasm undergoing superficial cleavage into cells. (*From Hegner: The Germ-cell Cycle in Animals. Copyright* 1914 *by the Macmillan Company. Reprinted by permission.*)

sooner or later passes the point at which such reversal is any longer possible. Obviously, the distinction between soma cells and germ cells cannot be sharply drawn. In the words of Hargitt (1925), whose researches on cœlenterates, amphibians and mammals are of particular interest in this connection, "germ cell origin is a question of cellular differentiation, and not of early ontogenetic segregation." This conclusion is equally evident in the case of plants, which develop reproductive cells from meristematic tissue often throughout a long life period, and which exhibit very commonly the production of such cells from dedifferentiated somatic tissues as well (see Beals, 1923).

With regard to the phenomena of heredity, therefore, we follow Weismann in attributing them largely to a genetically continuous and specifically organized germ-plasm, chiefly the chromatic nuclear substance; but we can no longer uphold his fundamental distinction between the germ cells and the soma.

*Origin of Heritable Variations.*—Geneticists are still in agreement with Weismann in accounting for new heritable variations chiefly as the results of hybridization (amphimixis) and alterations in the inheritance units (gene mutations) (Chapter XVII). They are not now inclined to see in such a process as "germinal selection" the underlying cause of gene modification, but little can at present be offered in its stead (p. 382).

Owing in part to a less sharp distinction between germ cells and somatic cells, as well as to an increased knowledge of hormone action, there is now somewhat less aversion to the idea of the inheritance of acquired somatic modifications; but it is still very difficult to obtain satisfactory evidence on this point, as reference to almost any textbook of genetics will show. It at least seems that if such inheritance were at all important in evolution, convincing evidence should be found on every hand. Induced modifications are frequently inherited, but one can rarely be sure that this is accomplished by the action of the soma alone upon the germ cells, and not by the action of the experimental factor upon the germ-plasm directly. The very general failure of acquired somatic modifications to be inherited is now usually attributed to the stability of the germ-plasm and the lack of a mechanism for the transfer to it, as it were, of such modifications, rather than to the isolation of the germ cells from the soma.

It is not yet possible to explain satisfactorily the preservation of incipient variations of no selective value and the tendency to vary along certain lines, phenomena attributed by Weismann to germinal selection. Very suggestive in this connection, however, is the fact of linkage. It is not at all improbable that "useless" small variations which would otherwise be swamped through crossing are retained because they are linked with characters of decided survival value. In this way the modification might be preserved until additional variations in the same direction give it selective value. Allusion has already been made to the fact that many species have been classified on the basis of characters which probably had nothing to do with the actual differentiation of those species (p. 409).

*Weismann's Contribution.*—The great contribution made by Weismann to the study of heredity may be summed up in three propositions: (1) the germ-plasm contains independent elements which may be substituted one for another without undergoing change; (2) a segregation of maternal and paternal factors, pair by pair, occurs at one period in the history of the germ cells; (3) the behavior of the chromosomes is specifically applicable to the problems of heredity (Morgan *et al.*, 1922). Upon these principles is founded the factorial hypothesis, now supported by a wealth of experimental evidence. Notwithstanding the abandonment of his theory of ontogenesis and the changes made in his theory of heredity, Weismann's influence on both cytology and genetics can never be forgotten, chiefly because of his emphasis on the need for careful studies of the nuclear mechanism at the critical stages of the life history, and upon the idea that this mechanism is in some way bound up with the phenomena of heredity. "It has been Weismann's service to place the keystone between the work of the evolutionists and that of the cytologists" (Wilson, 1900).

**Conclusions.**—In the foregoing pages have been mentioned some of the most important biological problems toward the solution of which cytology should make further contributions. Future investigation will probably reveal more fully by what means and to what extent the course of ontogenesis is controlled on the one hand by the operation of an inherited internal mechanism, and on the other by the action of environmental agencies. If the organism and the environment be conceived as constituting a single system producing the phenomena to be explained, a way may be found between the "Scylla of preformation and the Charybdis of epigenesis" (Conklin, 1913*b*). "In respect to a great number of characters," says Wilson (1925), "heredity is effected by the transmission of a nuclear preformation which in the course of development finds expression in a process of cytoplasmic epigenesis." Another important problem is to identify the unknown causes of the progressive modification of the nuclear mechanism, in order better to account for evolutionary advance.

It is obvious that no adequate solution of any of these problems can be reached until the physico-chemical constitution of protoplasm, particularly that of the germ-plasm or special inheritance material, has been more clearly disclosed. Only further research can show whether the physical basis of heredity will continue to be thought of as a system of peculiar discrete molecules or molecular complexes with a definite spatial arrangement, as is supposed in our current factorial theory, or will come to be looked upon as a single enormously complex chemical substance in which varying side-chains or other portions of the molecule are responsible for the variety of results observed. It is at any rate a striking fact that "in the Mendelian phenomenon we see a synthesis, splitting apart, and recombination of determinative factors that is singularly like that of chemical elements or radicals;" and it seems abundantly clear that "in the union of cytology and biochemistry lies our greatest hope of future advance" (Wilson, 1909*c*).

Whatever judgment may ultimately be rendered on the chromosome theory of heredity as outlined in these chapters, it must be agreed that the value of this theory in the present state of our knowledge can hardly be overestimated. Through its use an enormous number of the observed facts of heredity are being reduced to order. The painstaking investigation of the interrelationships of all the known heritable characters of even a single organism such as *Drosophila* cannot fail to be a great service to biological science. Its appeal to the cytologist, as Wilson states, is largely through the manner in which it seeks to make use of known mechanisms rather than entirely hypothetical processes. Those portions of the theory which are as yet little supported by the results of direct cytological observation at least have the virtue of affording a useful and graphic expression of the mutual behavior of hereditary characters. They serve to increase the number of observed phenomena statable in terms of order; and the reduction of experience to order and the statement of this order in simple formulæ, together with the search for new truth, constitute the principal tasks of science. If this work of correlation has been well done, the whole body of facts can readily be placed under another theoretical interpretation and described in a new set of terms should occasion require. In other words, if the gene hypothesis should fail to stand the test of verification, the formulæ derived through its use, *i.e.*, the laws epitomizing the observed behavior of inherited characters, would remain essentially the same notwithstanding the use of new terms for their expression.

With regard to the application of chiasmatypy to the problems of linkage and crossing-over, Wilson (1913) has said:

> This, admittedly, is a bold venture into a highly hypothetical region. Its justification is the pragmatic one that it "works." The hypothesis gives us the only intelligible explanation that has yet been offered for a series of undoubted facts; and it is certainly worthy of the most attentive further examination . . . We have much to gain and nothing to lose by the use of explanatory hypotheses that are naturally suggested by the facts and help us to formulate them for analysis, so long as such hypotheses are not allowed to degenerate into dogmas accepted as an act of faith, but are only used as instruments for further observation and experiment.

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